Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology

Biota of the Colorado Plateau


Wellsville Mountains, Utah. Photo © 1999 Ray Wheeler

From sparse desert communities growing in the region's rugged canyons to alpine tundra found atop the highest peaks, the biota of the Colorado Plateau is exceptionally diverse. This diversity can be attributed to the region's varied topography and its geographic position in the western United States. The Colorado Plateau is sandwiched between the Great Basin to the west, an arid region of alkaline basins and faulted mountain ranges, and the Rocky Mountains to the east, a lusher landscape of high peaks and rich forests. The region's flora and fauna thus has elements of each of these provinces as well as a significant number of endemic species that have evolved in areas of relative isolation atop the Plateau.

Elevation largely determines what type of biotic communities one may find in a given location, as temperatures generally decrease and precipitation increases as one moves upward. At 4000 feet in Canyonlands National Park one may be in a desert shrub community dominated by blackbrush or shadscale, while just to the east in the La Sal Mountains, but more importantly 5000 feet higher, rich grass-forb meadows and forests of quaking aspen dominate the landscape.

There are numerous other factors–recent, historical and ancient–that have affected the distribution of plant and animal species on the Colorado Plateau. Short and long-term climate change has played a large role in the development of the region's biota. In the last two millenia human activities have altered the region's environment. In the Four Corners area, the prehistoric Anasazi were so populous by the end of the 12th century that they must have had a significant impact on the landscape. Historically, among the Plateau's forests, the suppression of wildfire coupled with widespread grazing and intensive logging has led to many unforeseen changes, including changes in the composition and structure of forests as well as the spread of exotic species. Dam building and excessive pumping of groundwater have

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damaged many riparian ecosystems, which are critical to this dry region's plant and animal life. Though ongoing natural processes such as succession and climate change continue to alter the region's biota, the rapid changes seen today due to human activities are unprecedented in their impacts on the biota of the Colorado Plateau.

Research:

Packrat Midden Research in the Grand Canyon. On the Colorado Plateau the ice age (Pleistocene) vegetation of the Grand Canyon has been determined through the analysis of plant fossils preserved in caves and fossil packrat middens. Large changes occurred as the most recent ice age ended and the Holocene era began. Adapted by Kenneth L. Cole from his journal article.

Paleobotany and Paleoclimate of the Southern Colorado Plateau. The biota of the Colorado Plateau during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods was dramatically different from that seen today. Differences were primarily a result of major climate changes associated with the last major glacial period. This site examines the environment of the southern plateau during this time. Adapted by R. Scott Anderson from his journal article.

Native Americans and the Environment. A comprehensive survey of twentieth century environmental issues facing Native Americans on the Colorado Plateau and throughout the Southwest, including discussions of agriculture, logging, mining, grazing, water rights, and tourism. Adapted from a published journal article by David Rich Lewis.

Late Holocene Environmental Change in the Upper Gunnison Basin, Colorado. The Upper Gunnison Basin is a high elevation (3100 to 3600 m) region on the edge of the Colorado Plateau in southwestern Colorado. Its unusual ecological characteristics include an absence of plant and animal taxa that should occur here. Fossil and archaeological evidence indicates that many of the missing species existed in the Basin during the late Pleistocene to middle Holocene. Authored by Steve Emslie.

Fire-Southern Oscillation Relations in the Southwestern United States. A close linkage between fire and climate could diminish the importance of local processes in the long-term dynamics of fire-prone ecosystems. The structure and diversity of communities regulated by fire may have nonequilibrial properties associated with variations in global climate. Successful prediction of vegetation change hinges on a better understanding of climatically driven disturbance regimes and the relative contributions of regional versus local processes to community dynamics. Adapted from a journal article by Thomas W. Swetnam and Julio L. Betancourt.

Changed Southwestern Forests: Resource effects and management remedies. Over

150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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The Community Concept

Mixed aspen, spruce, and Douglas fir forest, south slope of Boulder Mt. on Utah's Aquarius Plateau. Photo © RayWheeler.

In the late 1880s, C. Hart Merriam surveyed the plant life of the San Francisco Peaks near Flagstaff, Arizona, for the federal Biological Survey. Merriam observed that from the top of the Peaks to the bottom of Grand Canyon, vegetative communities tended to occur along an elevation range. He sought to understand what factors influenced the distribution of the region's vegetation, and began to categorize distinctive vegetational belts or "life zones."

Ecologists and biogeographers still categorize ecological communities based on dominant vegetation, but modern classification systems are more complex than Merriam's. In this website we follow the "biotic communities" concepts of David E. Brown, which include both plant and animal life. (See reference below; for a list of biotic communities of the Colorado Plateau, see the left-side menu). For example, Abert's squirrel can be readily linked to its habitat of ponderosa pine forest while pinyon jays are primarily adapted to the region's expansive pinyon-juniper woodlands.

Modern ecology holds that all ecological communities are composed of individual species whose ecological tolerances happen to overlap, forming what appears to be a specific zone of vegetation. In other words, individual species have over time evolved their own ecological tolerances to different factors such as precipitation, soil types, shade, fires, temperature, etc. Though gambel oak and ponderosa pine commonly live in the same biotic community, if environmental conditions were to change each of these species would respond *individualistically*, and perhaps would end up in new, different communities. Paleoecological studies on the Colorado Plateau indicate that limber pine may have been one of the region's lower elevation

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pines in the past, living among juniper and pinyon-pine in a niche that is today occupied by ponderosa pine. Conditions have since changed, and limber pine is now predominantly seen growing in the subalpine conifer forest at high elevations. The pine has found a new niche, and is no longer a part of modern pinyon-juniper woodland or a ponderosa pine forest biotic communities.

For more information, see:
C Hart Merriam and the Life Zones Concept
Map of the Biotic Communities of the Greater Grand Canyon Region

Resource:

Brown, D. E. 1994. *Biotic communities of the Southwestern United States and northwestern Mexico.* University of Utah Press, Salt Lake City, 342 pp.

Research:

Paleobotany and Paleoclimate of the Southern Colorado Plateau. The biota of the Colorado Plateau during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods was dramatically different from that seen today. Differences were primarily a result of major climate changes associated with the last major glacial period. This site examines the environment of the southern plateau during this time. Adapted by R. Scott Anderson from his journal article.

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Alpine Tundra

Ancient limber pine in grassland near timberline in the Wellsville Mountains near Logan, Utah. Photo © 1999 Ray Wheeler.

True alpine tundra communities are found at only the highest elevations on the Colorado Plateau, generally above 12,000 feet. Here only specially-adapted tundra species are able to grow in the harsh climate. Winds are frequently strong, snowfall can be heavy, and the growing season is short, in some areas only thirty days annually. To avoid strong winds and retain precious heat absorbed from the ground or attained through solar radiation, tundra species are commonly small, ground-hugging plants, such as prostrate woody shrubs (commonly willows), herbs, lichens and mosses.

On the western edge of the Plateau, Mount Belknap and Delano Peak, atop the Tushar Plateau east of Beaver, Utah, support alpine tundra. The La Sal Mountains on the eastern fringe of the region are also tall enough at 12,000 feet to support this fragile alpine plant community. Though many of the other high plateaus of Utah, including the Markugunt, Aquarius, and Sevier, rise to over 11,000 feet and treeline, they are not quite high enough to support true tundra communities.

Near the very southern edge of the Colorado Plateau one can find alpine tundra on the uppermost slopes of the San Francisco Peaks just north of Flagstaff, Arizona. At 35° N, these peaks are the southernmost climatic alpine area on the continent north of the high volcanoes of central Mexico. Of over 80 species of plants found in this zone on the Peaks, almost half can be found in polar regions near the Arctic and on high summits north into Canada.

Geographically isolated areas often show endemism as the area serves as an "island" where species develop in a unique environment. Part of the San Francisco Peaks have been closed to travel to protect an endemic groundsel

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(*Senecio franciscanus*). The nearest alpine areas in southeastern Utah and southwestern Colorado are too far from the San Francisco Peaks for successful migration of many species.

Most alpine tundra ecosystems on the Colorado Plateau occur within national forests, but threats to these fragile ecosystems include localized recreational use, warming climates, and acid deposition. Changes in species plant composition and soil composition are of concern to alpine ecologists.

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Subalpine Conifer Forest

Bristlecone pine stand.

At elevations of 10,000 feet to about 11,500 feet on the Colorado Plateau, annual precipitation can be relatively high for this semi-arid region, from 30 to 35 inches a year. Much of this falls as snow during the cooler months, but a significant portion falls as heavy rains during the summer monsoon season, especially along the southern margin of the Plateau. Where lingering snowpacks keep the forest floor moist for much of the year, subalpine conifer forests dominated by Engelmann spruce and subalpine fir occur commonly as small, isolated mountaintop stands. Spruce-fir forests grade into bristlecone pine stands on some treeline sites, particularly on limestone substrates and drier south-facing slopes, and into mixed-conifer forests at lower elevations. Significant stands of quaking aspen occur in subalpine forests, particularly after fires.

In contrast to mixed-conifer and ponderosa pine forests found at lower elevations, natural fire is relatively uncommon in subalpine conifer forests. Some spruce-fir stands experience mixed fire regimes, with patchy crown fires occurring about every several hundred years, and more frequent surface fires occuring every 15 to 30 years. Overall, subalpine forests have probably been less altered by modern fire suppression than have the lower elevation forests. Livestock grazing has also had less impact, due to the natural lack of herbage in these forests.

Subalpine conifers are adapted to the strong winds and frigid temperatures atop the high peaks and tablelands of the region. The branches of the spruce and fir trees are short and brittle, so they grow close together to buffer the wind; both of these species have narrow, pointed crowns, which help shed snow. In contrast, the subalpine pines, limber and bristlecone, have more open crowns with flexible branches which help them withstand heavy snowfalls and blustery winds with less damage. Nevertheless,

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the uprooting and blowdown of subalpine trees by wind (windthrow) is a major natural disturbance factor. Windthrow is exacerbated where partial cutting of spruce-fir forest exposes remaining old trees to new wind stresses. Logging operations also contribute to outbreaks of spruce beetles, since these insects prefer downed trees. In areas where spruce-fir stands have been clearcut, regeneration has been a problem. Projected climate changes might eliminate some subalpine forests from isolated mountain ranges.

Lack of aspen regeneration has also been a consequence of modern fire suppression, and conifer understories are now widely overtopping aspen stands. Elk herbivory on aspen sprouts also retards regeneration on small burns or clear-cuts. Between 1962 and 1986, the area of aspen stands declined by 46% in Arizona and New Mexico. Many aspen forests in the Southwest are now composed of trees more than 100 years old. These trees are particularly susceptible to increased insect and disease problems. Without major fires, aspen stands will continue to decline, although aspen clones are able to persist in a suppressed state in the understories of conifer forests for many years. The high probability of intense fires in southwestern conifer forests in the coming decades suggests that new aspen stands will develop again soon, changing their status from declining to increasing.

Research:

Paleobotany and Paleoclimate of the Southern Colorado Plateau. The biota of the Colorado Plateau during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods was dramatically different from that seen today. Differences were primarily a result of major climate changes associated with the last major glacial period. This site examines the environment of the southern plateau during this time. Adapted by R. Scott Anderson from his journal article.

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Quaking Aspen Forest

Old-growth aspen forest, south slope Boulder Mountain, Aquarius Plateau. Photo © 1999 Ray Wheeler

The widespread distribution of quaking aspen (*Populus tremuloides*) forests on the region's high plateaus and mountain ranges and their importance to many wildlife species make these forests a significant biotic community on the Colorado Plateau. Large, nearly pure stands of aspen can be seen on the Markagunt, Aquarius, Pansaugunt, and Wasatch Plateaus of central and southern Utah and in the La Sal Mountains on the eastern border of the state. Grand Mesa and the Uncompaghre Plateau in far western Colorado also support extensive aspen forests. Further south, aspen is abundant in the White Mountains, on the Kaibab Plateau, and on the San Francisco Peaks in Arizona. Aspen is most commonly found between 7500 and about 10,500 feet on the Colorado Plateau, particularly on well-watered south-facing slopes.

In the La Sal Mountains of southeastern Utah, a zone of quaking aspen, interspersed with grass and forb meadows, occupies an elevational belt from 8500 to 10,000 feet. These pure aspen forests may actually represent "climax" vegetation, as Douglas-fir, white fir, and blue spruce are absent. It may be too dry to support these conifers, but it appears that soil type may be a more important factor. The aspens grow on soil derived from shale, and the conifers may have difficulty competing with aspen on that soil type.

The understory of most aspen communities is luxuriant when compared with those of associated coniferous forests. The combination of more abundant sunlight and favorable moisture conditions in many stands often leads to a rich forest floor of grasses, forbs, and shrubs. Drier groves are characterized by an herbaceous layer consiting mostly of grasses, with some wildflowers and medium-sized shrubs such as ninebark or cinquefoil. Wetter forests have an abundance of wildflowers,

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including meadowrue, arnica, lupine, and paintbrush, and sometimes a thicker shrublayer consisting commonly of snowberry or wild rose.

Aspen grow in distinct clones, which often can be distinguished in early summer when the trees are leafing out or during the fall when clones change different colors or at different times. Aspen stands are usually moist and do not readily burn, but the tree has thin bark and is easily killed by a light fire. However, after a fire aspen can readily re-sprout or sucker from shallow lateral roots. This is an important advantage over competing conifers which may have to reseed.

Although aspen is considered a climax species on some sites, it is usually seral to conifers. This replacement is gradual and can take from 100 to 200 or more years. If an aspen stand is within a mixed conifer forest, conifers can become established within a single decade. Because aspen stands are so different from conifer stands, they are very important for landscape diversity and wildlife habitat. Although aspen stems are short lived and snags do not stand long, the wood is soft, often decayed, and therefore useful to cavity-dependent species. Young sprouts are heavily browsed by elk and deer.


Late successional aspen forest. Photo by Keith Pohs

Aspen stands are in decline on the Colorado Plateau. The U.S. Forest Service extimates that between 1962 and 1986, aspen stands have declined by 46% in Arizona and New Mexico. The combination of modern fire suppression and a steady increase in elk herbivory has prevented aspen regeneration in many forests; conifer understories are now widely overtopping aspen stands. Aspen clones are able to persist in a suppressed state in the understories of conifers for many years, but without major fires aspen stands will continue to decline. The high probability of intense fires in southwestern conifer forests in the coming decades suggests that new aspen stands will develop again soon, changing their status from declining to increasing.

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Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

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Mixed-Conifer Forest

Dense mixed-conifer forest. Under a natural fire regime, these forests are often more open. Photo by Keith Pohs.

On the Colorado Plateau mixed-conifer forests generally occur at elevations from about 8000 feet to 10,000 feet, where annual precipitation is from 25 to 30 inches annually. In contrast to the ponderosa pine forest growing at slightly lower elevations, the mixed-conifer forest is comparatively lush and much more diverse. Depending on location, Douglas-fir, white fir, limber pine (in the north), blue spruce, and less commonly southwestern white pine form mixed stands in this community, with ponderosa pine joining the mix on warmer slopes. Blue spruce is common in moist areas on many of the high plateaus of central and southern Utah, while limber pine is a major component of mixed-conifer forests on the San Francisco Peaks near Flagstaff, Arizona. Quaking aspen, along with Gambel oak, is prominent in these forests following disturbances.

Under natural conditions the relatively open nature of the mixed-conifer forest coupled with the rich, moist soil found at these elevations allows for the development of a diverse understory of forbs, grasses, and shrubs. Understory conditions vary widely, from dry, open-canopy forests with grassy undergrowth on open slopes and ridges to moist, closed-canopied stands dominated by numerous herbaceous plants in the canyons and ravines. A popular zone for wildlife due to the abundant forage, black bears, mule deer, and elk can be quite common.

Fire histories in mixed-conifer forests vary with forest composition, landscape characteristics and human intervention. Until the late 1800s when grazing and fire suppression policies vastly reduced widespread fires, fire regimes included frequent surface fires to infrequent, patchy crown fires with return intervals of about 10 years. In the absense of fire these forests have undergone

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major changes in structure and species composition throughout the American west.

Ponderosa pine was once codominant in many mixed-conifer forests with relatively open stand structures, but fire suppression has allowed the development of dense sapling understories, with regeneration dominated by the more fire-sensitive Douglas-fir and white fir. Forest stand inventory data from Arizona and New Mexico show an 81% increase in the area of mixed-conifer forests between 1962 and 1986. Herbaceous understories have been reduced by denser canopies and needle litter, and nutrient cycles have been disrupted. Heavy surface fuels and a vertically continuous ladder of dead branches have developed, resulting in increased risks of crown fires. As these forests become reduced or fragmented, local endemic plants may become threatened or endangered.

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Biotic Communities of the Colorado Plateau

Biota

Ponderosa Pine Forest

Restored ponderosa pine forest near Flagstaff, Arizona. Photo by Keith Pohs.

Forests of ponderosa pine cover many of the higher mesas and mountains of the Colorado Plateau from 6000 feet to about 8000 feet in elevation. On higher terrain above 6500 feet in the southern part of the region, including the Kaibab Plateau and atop the Mogollon Rim, ponderosa pine often forms nearly pure stands covering tens of thousands of acres. The forest stretching from near Flagstaff along the rim to the White Mountains region is the largest ponderosa pine forest on the continent.

The predominant form of the pine throughout the Colorado Plateau is the three-needled, Rocky Mountain ponderosa pine (*Pinus ponderosa var. scopulorum*). Gambel oak (*Quercus gambelii*) is a common associate of ponderosa pine at lower elevations in the forest along with New Mexico locust (*Robina neomexicana*). At higher elevations, associates include southwestern white pine (*Pinus strobiformis*), Rocky Mountain Douglas-fir, (*Pseudotsuga menziesii var. glauca*), Rocky Mountain white fir (*Abies concolor var. concolor*), and quaking aspen (*Populus tremuloides*). Common understory plants include grasses such as Arizona fescue and mountain muhly and forbs such as lupine. Buckbrush, cliffrose, currant, and apache plume can be seen growing beneath the tall, spreading crowns of the pines as well.

Ponderosa pine forests have a remarkably dynamic history on the Plateau. Evidence found in packrat middens, alluvial and cave sites, and in ancient pollen samples collected from lake, bog, and wetland sites throughout the region reveal almost no ponderosa pine during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods. Instead, areas that are today vast forests of ponderosa were thickly-forested with a mixed assortment of different conifers, including subalpine species such as Engelmann spruce which today grow only at

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the highest elevations, thousands of feet above their former range. Differences are primarily a result of major climate changes associated with the end of the last major glacial period. Studies indicate that during the middle-Wisconsin temperatures on the Colorado Plateau were approximately 3-4 degrees Celsius cooler than they are today, and perhaps 5 degrees cooler during the late-Wisconsin.

Even during the Holocene of the last 11,000 years B.P., evidence suggests that ponderosa pines were more widespread at lowel elevation during the early to middle Holocene, only to contract their ranges in the late Holocene. Fire is a critical factor in the ecology of ponderosa pine, so relatively subtle changes in climate such as the timing of seasonal rains and their associated lightning strikes, may have a larger impact on ponderosa pine than on some other western conifers.

Today, the typical climate of a ponderosa pine forest includes an adequate, annual amount of moisture for good vegetative growth and conditions favorable for frequent early summer fires. Winters are relatively mild (average slightly above 30° F) and precipitation as snow saturates the soil. The spring dry season is accompanied by increasing air temperatures, low humidity, and persistent winds. The drought is broken in early to mid-July with the development of almost daily thunder and lightning storms, especially along the southern edge of the Colorado Plateau in areas such as the Mogollon Rim and White Mountains. July and August are the wettest, warmest months. A second dry season occurs in the fall. This climatic pattern is particularly conducive for development of a pine-grass savanna maintained by frequent surface fires.

Before European settlement, widespread surface fires that occurred every 2-15 years favored grasses and limited pine densities. Early explorers described majestic, open stands with rich grasses and occasional shrubs beneath, as young ponderosa seedlings were often killed by the low-intensity fires while mature pines, with their thick yellowish red bark, were only scarred. The effects of grazing and fire suppression since the late 1880s on ponderosa pine forests have been profound, including a shift to forests with very high tree densities, which in turn has contributed to destructive forest fires. Separate web pages give more detail on ponderosa pine fire ecology and reintroduction of fire to forest ecosystems. Two longer research essays, Changed Southwestern Forests: Resource effects and management remedies, and Restoring Ecosystem Health in Ponderosa Pine Forests of the Southwest are also available in this website.

The tassel-eared Abert's squirrel is a distinctive inhabitant of ponderosa pine forests on the central and southern Colorado Plateau. Few mammal species are so closely tied to a particular tree as this squirrel is to ponderosa pine. The bushy-tailed squirrel uses the tree for nesting, shelter, and food, feeding on the ponderosa's seeds and the tree's cambium layer. Abert's squirrels can be quite acrobatic, sometimes jumping 40 feet or more

Photograph courtesy of W. Sylvester Allred, Northern Arizona University

to the ground unharmed.

Mule deer and rocky mountain elk also live among the pines along with smaller mammals including numerous chipmunks and voles. Several bird species are commonly seen in this pine habitat, including Steller's jay, brown creeper, white and red-breasted nuthatches, juncos, red-shafted flicker, and the colorful western tanager, a summer resident from the tropics.

Follow these links to:
Ponderosa Pine Fire Ecology
Reintroduction of Fire to Forest Ecosystems

Research:

Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Restoring Ecosystem Health in Ponderosa Pine Forests of the Southwest. Restoration of ecosystem structure and reintroduction of fire are necessary for restoring rates of decomposition, nutrient cycling, and net primary production to natural, presettlement levels. The rates of these processes will be higher in an ecosystem that approximates the natural structure and disturbance regime. Adapted from a published journal article by W. Wallace Covington *et al*.

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Biotic Communities of the Colorado Plateau

Biota

Montane Chaparral/Scrub

Fall colors of montane chaparral/scrub in the Wellsville Mountains, Utah. Photo © 1999 Ray Wheeler

Montane chaparral or montane scrub communities occur on the Colorado Plateau generally at elevations of 6000 to nearly 8000 feet. They occur most commonly in the central and northern parts of the region, and usually replace ponderosa pine or mixed-conifer forests.

These community-types tend to be found on steep slopes where there is poor soil development and cold microclimates. Annual precipitation between 15-21 inches tends to be lower than the mean for these elevations, and is generally spread throughout the year.

Composed primarily of Gambel oak and bigtooth maple, montane chaparral/shrub communities may also include black sagebrush and curleaf mountain mahogany among other species. Occasional patches are common at middle elevations on the high tablelands of southern and central Utah. In the La Sal Mountains, a community composed primarily of Gambel oak and mountain mahogany nearly replaces ponderosa pine in a mid-elevation belt surrounding the range.

Mule deer depend on this vegetation-type for food, especially in the winter, as do many resident bird species. Excessive grazing of livestock has modified much of this biotic community. Native grasses are often scarce, replaced by Kentucky blue-grass and non-native bromes such as cheatgrass.

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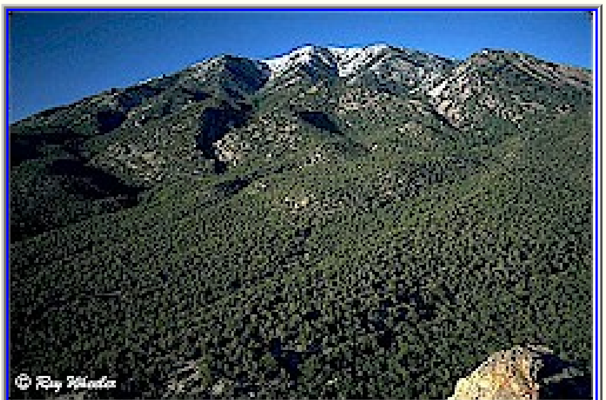
Biota

Pinyon-Juniper Woodland



Pinyon-juniper woodland on the west face of Mt. Pennell in the Henry Mtns.
Photo © 1999 Ray Wheeler

Pinyon-pine and juniper woodlands are widespread on the Colorado Plateau between about 5000 feet to 7000 feet in elevation. 11.4% of New Mexico, or about 3.6 million hectares, consists of pinyon-juniper habitat. In Arizona there are over 5 million hectares of "P-J," as this "elfin" or "pygmy" woodland is often called.

While the U.S. Forest Service distinguishes 32 pinyon and 23 juniper plant communities,
Colorado pinyon pine (*Pinus edulis*) is the most common pine species in this woodland type, and Utah juniper (*Juniperus osteosperma*) is the most common juniper. One-seed (*J. monosperma*), Rocky Mountain (*J. scopulorum*), and alligator (*J. deppeana*) junipers can be abundant in different areas of the Plateau.

Annual precipitation is typically from 10 to about 15 inches in pinyon-juniper woodlands, and tree species in these communities have evolved both drought and cold resistance. Pinyons dominate at higher elevations, and tend to form more closed-canopied stands that exhibit forestlike dynamics and species composition, commonly including a significant shrub component of oaks and alderleaf, mountain mahogany and limited grasses. Juniper tends to grow at lower elevations and in more arid areas as its scaled foliage allows it to conserve water more effectively than pinyon pine. Juniper-dominated woodlands tend to include open savannas of scattered trees without a significant shrub component, except in areas where big sagebrush has become dominant as a consequence of overgrazing. There are relatively few vertebrates endemic to pinyon-juniper woodlands, but there are significant levels of biodiversity in less prominent organisms such as herbaceous vegetation and soil organisms.

The long history of livestock grazing in many pinyon-juniper woodlands on the Colorado Plateau has both diminished and altered herbaceous vegetation, leading

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Utah Juniper (the tree in the right foreground) with big sagebrush (gray-green shrubs on the left). Photo courtesy [USGS/BRD](#).

to widespread desertification of understory conditions. Although there is little firm documentation of woodland fire histories, many researchers believe that year-round grazing since the late 1800s suppressed former fire regimes; surface fires could no longer spread though the bare interspaces between the trees. Accelerated precipitation runoff and soil erosion commonly occur in these areas, leading to significant, permanent losses of site productivity and erosive watershed conditions. Major vegetative changes include decreases in cool-season grasses, and increases in grazing-resistant plants such as snakeweed and big sagebrush.

Woodland communities have expanded considerably over the course of this century in many parts of the Colorado Plateau. Tree densities have increased, and junipers and pinyon pines have expanded upslope into ponderosa pine forests and downslope into grass and shrub communities. Densities have increased in some areas to the point that larger proportions of pinyon-juniper woodland can now support crown fires. For a discussion of the causes of this type of woodland expansion, see the research essay, [Where Have All the Grasslands Gone?](#)

Snowcovered chaining project - Dark Canyon Plateau, Utah. Photo © 1999 [Ray Wheeler](#).

"Chaining," or mechanical removal of woodlands by land management agencies, has been commonly used in an effort to convert woodlands to grasslands for livestock. For example, about 600,000 hectares of pinyon-juniper woodlands were mechanically treated in Arizona during the 1950s and early 1960s, as were about 223,000 hectares of woodland on U.S. National Forests alone between 1950 and 1985. This process, though effective in uprooting and killing the trees, is damaging to other community species and may be less beneficial than other management strategies. Its use has been greatly reduced since the 1970s. Harvests for fuelwood also peaked in the 1970s, when harvest levels proved unsustainable in some areas. Current management policy by the U.S. Forest Service focuses more attention on active management of woodlands to restore less erosive watershed conditions.

Research:

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

Packrat Midden Research in the Grand Canyon. On the Colorado Plateau the ice age (Pleistocene) vegetation of the Grand Canyon has been determined through the analysis of plant fossils preserved in caves and fossil packrat middens. Large changes occurred as the most recent ice age ended and the Holocene era began. Adapted by Kenneth L. Cole from his journal article.

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Biotic Communities of the Colorado Plateau

Mountain Grasslands and Meadows

Aspen groves and mountain grasslands; east slope of Thousand Lake Mountain, Fishlake Plateau, Utah. Photo © 1999 Ray Wheeler.

Subalpine and montane grasslands and meadows occur on many of the high plateaus and isolated mountain ranges of the Colorado Plateau. Annual precipitation ranges from 30 to 45 inches, with almost 50% occurring during the summer monsoon season. These communities commonly form on flat areas with poorly-drained soils or on high, often east or south-facing, windswept ridges. There is commonly an abrupt transition between surrounding forests and these grasslands, producing an "edge effect" of high biological productivity. These grasslands and meadows are important to many species, including several large and small mammals, among them elk, deer, pronghorn, gophers, and voles, as well as numerous birds, including wild turkey and western bluebird.

Mountain grasslands are generally found between 7,500 and 8,500 feet in elevation on the Colorado Plateau. When healthy, they are commonly composed of abundant perennial bunchgrasses, including Arizona fescue, needlegrasses, or wheatgrasses, mixed with forbs such as yarrow, larkspur, or fleabane. While grasslands occur in uplands, mountain meadows occur in drainages, and are characterized by herbaceous plants, grasses, sedges and rushes.

Subalpine grasslands occur above 8,500 feet in the White Mountains, on the Kaibab Plateau, in the Chuska Mountains, and on the San Francisco Peaks in Arizona. The far northeastern portion of the Aquarius Plateau in southern Utah, termed Boulder Top, includes numerous lakes, wet meadows, and extensive subalpine grasslands. In the La Sal Mountains of southeastern Utah, montane grass-forb meadows are common with quaking aspen forests occurring along an elevational belt from 8500 to about 10,000 feet.

Agents of Biotic Change

Since the late 1800s these higher elevation grasslands and meadows have been used for summer forage for cattle and sheep ranchers. Excessive stocking numbers on these once lush mountain meadows has resulted in widespread ecological degradation in many areas, predominantly from overgrazed plots and introduction of livestock too early in the season, when native grasses are vulnerable to damage. Grazing by livestock tends to lead to an increase in less palatable species, such as forbs, and a decrease in overall vegetative cover, leading to more rapid runoff of precipitation and erosion of soils.

The suppression of wildfire combined with overgrazing has led to an overall decrease in mountain grassland habitats throughout the highlands of the Colorado Plateau. Woody species such as sagebrush in the lower montane zones and conifers and aspen at higher elevations have rapidly invaded once expansive mountain meadows throughout the region, particularly over the last 50 years. Conifers, especially blue spruce, are invading meadow margins in many areas. Arroyo cutting, caused by elimination of beavers and continued livestock grazing, has dried out many meadow sites. Increased tree densities in surrounding forests due to fire suppression and grazing may be further contributing to the problem by transpiring water that previously kept many meadows moist.

Burgeoning elk populations are inhibiting land managers' attempts to improve grassland conditions by reducing livestock numbers. Studies in the Jemez Mountains of New Mexico have found that moist meadows are now often dominated by nonindigenous plants such as Kentucky bluegrass, white clover and dandelion.

Research:

Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology
Ponderosa Fire Ecology
Tamarisk Invasion

Biotic Communities of the Colorado Plateau

Biota

Semi-arid Grasslands and Shrublands

Grassland north of Flagstaff, AZ. Photo by John Grahame

Below 6,000 feet in the cool-temperate region of southern Utah, northern Arizona, and northwestern New Mexico several different types of native grasslands were once common. The two most dominant were a Great Basin grassland, typical of the more western, central, and northern regions, and a Plains grassland, which is confined to the southeastern part of the region. Plains grasslands are commonly dominated by Blue Grama or other gramas that extend into the area from southern Colorado and northwestern Texas. Great Basin grasslands are dominated by Galleta Grass and Indian Rice Grass and reach down to the Colorado Plateau from the northwest. Both types intergrade downslope with semi-arid scrub communities and upslope with pinyon-juniper woodlands.

A large transitional area between the two types occurs in north-central Arizona and extreme southern Utah. Most of the cold-tolerant, cool-season bunch grasses that are native to these grasslands are most productive during spring and early summer, and once existed in a mosaic with deep-rooted shrubs. Until the late 1800s and the coming of the railroad and the cattle industry, the only large animals to graze these lands were pronghorn antelope. It took only 10-15 years of overgrazing by cattle near the end of the last century to extensively alter these ecosystems. The native bunchgrasses, not generally tolerant of grazing, sustained high mortality when grazed heavily in spring. Wildfires, once common in these grasslands, are far less frequent today as grazing has left less residual grass to carry fires and land management agencies maintain fire suppression policies. Both grazing and fire suppression favored shrub species over grasses and accelerated soil erosion. Site conditions have been permanently altered, and Eurasian annual grass species such as cheatgrass have aggressively colonized vast areas.

Agents of Biotic Change

No visitor to these cold-temperate regions can fail to be impressed by the omnipresence of big sagebrush, a hardy, cold-tolerant shrub that shapes the ecosystems it dominates. Its expansion on the Colorado Plateau has been remarkable. Though big sagebrush tends to be widely spaced with herbaceous plants and grasses living beneath them, the intershrub spaces are barren or contain microphytic crusts composed of lichens and algae. The shrubs concentrate water and nutrients to form islands of fertility that are not easily altered. The current mosaic of shrublands dominated by big sagebrush, and grasslands dominated by cheatgrass, is in large part a reflection of continuing desertification of the Colorado Plateau. The pre-settlement mosaic of cool-season bunch grasses and deep-rooted shrubs may now be one of the rarest ecosystems in the Southwest.

Grazing continues to be widespread in these grasslands, and the colonization by cheatgrass and expansion of big sagebrush at the expense of native perennial grasses is expected to continue. Extensive amounts of land are also being converted to agricultural production, especially in the Four Corners area where Arizona, Colorado, New Mexico and Utah meet. Once these ecosystems are converted, there is only limited potential for conversion to native grasslands, either mechanically or by removal of livestock.

Research:

The social and ecological consequences of early cattle ranching in the Little Colorado River Basin. Examines the early development of cattle ranching in the Little Colorado River Basin, the various factors which contributed to overgrazing in the region, and the pervasive effects that early commercial cattle ranching had on the local environment.

Native Americans and the Environment. A comprehensive survey of twentieth century environmental issues facing Native Americans on the Colorado Plateau and throughout the Southwest, including discussions of agriculture, logging, mining, grazing, water rights, and tourism. Adapted from a published journal article by David Rich Lewis.

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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Biotic Communities of the Colorado Plateau

Biota

Mountain Wetlands

Boulder Top subalpine lake on Utah's Aquarius Plateau. Photo © Ray Wheeler

Interspersed among the region's high-elevation forests and mountain grasslands are marshes or cienegas and other similar aquatic environments. Though some areas have an abundance of surface water, such as the White Mountains of Arizona and a few of the high plateaus of Utah, in other areas such as the Kaibab Plateau surface water is limited by limestone or porous volcanic bedrock, despite adequate precipitation. Natural high-elevation wetlands on the plateau include Mormon and Stoneman Lakes along the Mogollon Rim in Arizona and the many subalpine lakes of the Boulder Top area of the Aquarius Plateau in southern Utah.

Common species living in areas of perennial or near-perennial surface water at middle and high elevations include cattail, bulrush, sedges, waterweed, spike rushes, quaking aspen, Colorado blue spruce, currants, shrubby cinquefoil, elderberry, and several types of willows. Pond weeds and manna grasses are common submergent plants. Principal waterfowl species include mallard, pintail, cinnamon teal, ruddy duck, and redhead. Taller emergent plants such as bulrush provide nesting sites for American bittern, yellow- and red-headed blackbirds, and marsh wren.

Beaver probably once played an important role in creating and maintaining mountain wetland areas. Tree cutting and dam building by beavers trap alluvial sediments, provide opportunities for new plant growth, and increase the diversity of wildlife habitats. The loss of beavers and their dams to overharvesting by early trappers probably degraded many if not most of these wetlands, contributing to arroyo-cutting and gullying of the landscape. As channels cut deeper water tables were lowered and surface sediments began to dry out; gradually, the vegetation becomes composed of plants tolerant of drier conditions.

Agents of Biotic Change

Resources:

Almand, J., and W. Krohn. 1979. The position of the Bureau of Land Management on the protection and management of riparian ecosystems. Pages 259-361 in R. Johnson and F. McCormick, technical coordinators. *Strategies for protection and management of floodplain wetlands and other riparian ecosystems*. Proceedings of the symposium, 11-13 December 1978. U.S. Forest Service General Technical Report WO-12, Washington, D.C.

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Biotic Communities of the Colorado Plateau

Biota

Riparian Areas

Riparian habitats, at the interface between wet and dry systems, are defined by the plants that inhabit them. Riparian plants depend on an intact hydrological regime where groundwater is maintained and natural surface flows occur. On the Colorado Plateau, many hydrological regimes are characterized by annual cycles of flooding and minimal flows, which determine sediment availability.

Beaver Creek Canyon, east slope of La Sal Mountains, Utah. Photo © Ray Wheeler.

Several regionally significant rivers, including the San Juan, Escalante, Sevier, Little Colorado, Green, and Colorado, cut through the stark mesas and broad plains of the Colorado Plateau. Continuous corridors of riparian vegetation once covered hundreds of miles along desert and mountain rivers. Besides forested riparian communities, there were riparian shrublands, marshlands, and grasslands. These plant communities were found at elevations from high wet meadows and cienegas, to tree-banked streams, to slack water sloughs and marshes–the alpine, montane, and floodplains-plains riparian ecosystems.

Along many rivers and creeks on the Colorado Plateau at middle elevations, from about 5000 feet to nearly 8,000 feet, several broadleaf trees commonly form riparian gallery forests or woodlands. These communities are especially well-developed where environmental conditions permit a mix of some lower-elevation species with some higher-elevation species. Common native trees and shrubs, depending on location and elevation, include narrowleaf cottonwood (*Populus angustifolia*), box-elder (*Acer negundo*), bigtooth maple (*Acer grandidentatum*), Rocky Mountain maple (*Acer glabrum*), water birch (*Betula occidentalis*), aspen (*Populus tremuloides*), thin-leaf alder (*Alnus tenuifolia*), New Mexico locust (*Robinia neomexicana*), Scouler willow (*Salix scouleriana*), and arroyo willows

Agents of Biotic Change

(*Salix lasiolepis*).

At higher elevations a large proportion of the Colorado Plateau's streams pass through the upland montane forests of mixed-conifer and ponderosa pine communities. The riparian zones themselves are usually narrow, often following relatively steep stream channels in restricted valleys. White fir and blue spruce are the common conifers in and adjacent to these montane riparian ecosystems. The streams usually flood from snowmelt in the spring, and many riparian species depend on over-bank flooding for seed transport and burial in fresh, fertile alluvial sediments. Seed shedding and flooding tend to coincide.

Although the riparian habitats of these rivers and their tributaries represent less than 1 percent of the total acreage of public lands in the 11 western states, about 72% of all reptiles, 77% of all amphibian species, 80% of all mammals, and 90% of all bird species which occur regularly in the Colorado Plateau region routinely use riparian areas for food, water, cover or migration routes. About 30% of the region's bird species use wetlands and other aquatic areas to the exclusion of upland habitats. Wetland and riparian habitats also support a disproportionate number of species that are of concern because they migrate to neotropical areas, have small continental populations, or are declining.

Since settlement by Europeans, riparian forests of all types have suffered enormous declines due to destruction, conversion to other uses, or significant degradation in structure, function, or composition. Non-native saltcedar or tamarisk (*Tamarix ramosissima*) is now a dominant riparian shrubby tree in the Colorado River basin below 6,000 feet, spread rapidly throughout the system via wind-dispersed seeds. Overall, a 90% loss of presettlement riparian ecosystems has occurred in Arizona and New Mexico. For an essay on the causes and consequences of riparian loss and degradation, click here.

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

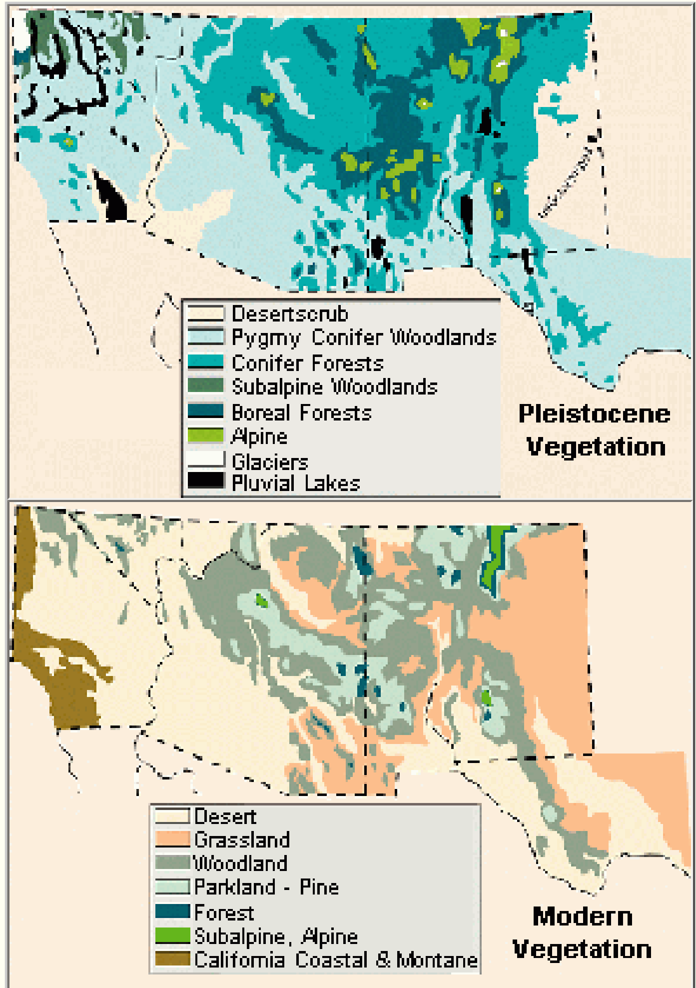
Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology

Biotic Communities of the Colorado Plateau

Paleocommunities

The biotic communities seen today on the Colorado Plateau are only the most recent communities which have evolved; plants and animals continually adapt to changing environmental conditions. Plant or animal associations commonly seen today may not have occurred in the past, while different communities may have existed in the past which today are rarely if ever seen. Evidence for these significant changes is found in packrat middens, alluvial and cave sites, and in ancient pollen samples collected from lake, bog, and wetland sites throughout the region.



Figures from Allen, C.D. et al., Landscape Changes in the Southwestern United States: Techniques, Long-term Data Sets, and Trends, available at http://biology.usgs.gov/luhna/chap9.html

These differences in biotic communities over time are primarily a result of climate change. For example, studies indicate that during the Pleistocene middle-Wisconsin time period (50,000-27,500 B. P.), temperatures on the Colorado Plateau were approximately 3-4 degrees Celsius cooler than they are today, and perhaps 5 degrees cooler during the late-Wisconsin (27,500-14,000 B. P.). There is also some evidence that these time periods were wetter as well, meaning that the conditions for growth were very different from what we observe today.

Information about former plant distributions can be synthesized into regional

Ponderosa Fire Ecology
Tamarisk Invasion

Agents of Biotic Change

vegetation maps through time. The maps on this page compare modern and late Pleistocene vegetation on the southern Colorado Plateau. From Pleistocene to modern, note the great contraction of alpine tundra and spruce-fir boreal forests in the southern Rockies, and the elimination of pluvial lakes that once filled large areas in the Great Basin region west of the Plateau.

One of the more remarkable changes is the expansion of ponderosa pine during the last 10,000 years onto much of the Colorado Plateau between about 6000-8000 feet in elevation. During the Pleistocene, ponderosa pine was probably limited to latitudes south of the transect from Albuquerque to Flagstaff. Areas that are today extensive ponderosa parklands and woodlands were thickly-forested with a mixed assortment of different conifers well into the early Holocene. These included subalpine species such as Engelmann spruce which today grow only at the highest elevations, thousands of feet above their former range. In what must be considered a remarkably short time ecologically, ponderosa pine has expanded its range from the Mexican highlands to the Canadian border, and is now the dominant large conifer of the Colorado Plateau.

Research:

Packrat Midden Research in the Grand Canyon. On the Colorado Plateau the ice age (Pleistocene) vegetation of the Grand Canyon has been determined through the analysis of plant fossils preserved in caves and fossil packrat middens. Large changes occurred as the most recent ice age ended and the Holocene era began. Authored by Kenneth L. Cole.

Paleobotany and Paleoclimate of the Southern Colorado Plateau. The biota of the Colorado Plateau during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods was dramatically different from that seen today. Differences were primarily a result of major climate changes associated with the last major glacial period. This research essay examines the environment of the southern Plateau during this time. Adapted by R. Scott Anderson from his 2000 journal article.

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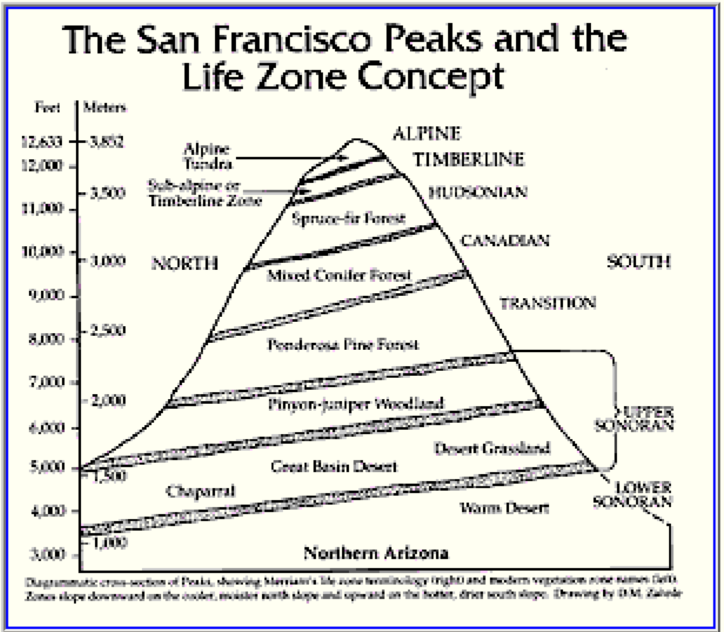
Elevational Range

On the semi-arid Colorado Plateau elevation is an important factor in determining what assemblages of species or biotic communities occur in a given location. As one moves upward in elevation temperatures generally decrease and precipitation increases.



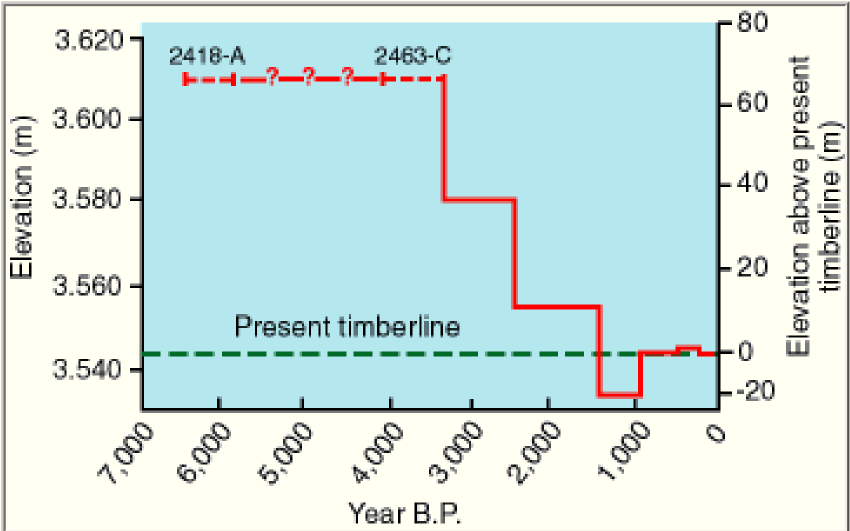
[C. Hart Merriam's Life Zones](). Drawing by D.M. Zahnie

C. Hart Merriam's studies of the biota from the top of the San Francisco Peaks at 12,600 feet to the bottom of Grand Canyon at less than 3000 feet impressed upon the scientific community the importance of elevation and latitude on the location of biotic communities. Subsequent studies have revealed that elevation is only one of a complex of factors that determine the presence or absence of species, populations, and communities. These factors include aspect (i.e., which direction the slope is facing), wildfire history and frequency, and soil type.

Evidence from paleoecological studies suggest that elevational ranges for particular species have fluctuated over time in response to major climatic changes. For example, today on the San Francisco Peaks, subalpine forests of Engelmann spruce generally grow from 9500 to about 11,500 feet (see figure above). At the height of the last glaciation (about 20,000 years ago) this species grew as low as 7000 feet, and probably not much higher than 9000 feet, far lower in than its current distribution. Timberline in the region, which today is about 12,000 feet, was apparently much higher during much of the middle Holocene (7500-3000 years ago) and a bit lower than today about 1500 years ago (see figure below). These significant fluctuations are a result of species responding to the dynamic nature of the earth's climate over time.

Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology
Ponderosa Fire Ecology
Tamarisk Invasion

Agents of Biotic Change



Source: Robert S. Thompson and Katherine H. Anderson "Past Climate and Vegetation Changes in the Southwestern United States" http://geochange.er.usgs.gov/sw/impacts/biology/pastclim/

Research:

Packrat Midden Research in the Grand Canyon. On the Colorado Plateau the ice age (Pleistocene) vegetation of the Grand Canyon has been determined through the analysis of plant fossils preserved in caves and fossil packrat middens. Large changes occurred as the most recent ice age ended and the Holocene era began. Adapted by Kenneth L. Cole from his journal article.

Paleobotany and Paleoclimate of the Southern Colorado Plateau. The biota of the Colorado Plateau during the middle (50,000-27,500 B.P.) and late (27,500-14,000 B.P.) Wisconsin time periods was dramatically different from that seen today. Differences were primarily a result of major climate changes associated with the last major glacial period. This site examines the environment of the southern plateau during this time. Adapted by R. Scott Anderson from his journal article.

Late Holocene Environmental Change in the Upper Gunnison Basin, Colorado. The Upper Gunnison Basin is a high elevation (3100 to 3600 m) region on the edge of the Colorado Plateau in southwestern Colorado. Its unusual ecological characteristics include an absence of plant and animal taxa that should occur here. Fossil and archaeological evidence indicates that many of the missing species existed in the Basin during the late Pleistocene to middle Holocene. Authored by Steve Emslie.

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/ Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation

Biotic Communities of the Colorado Plateau

Biota

C. Hart Merriam and the Life Zones Concept

The idea of mapping how plants and animals are distributed across landscapes neither began nor ended with C. Hart Merriam, but Merriam's work at the end of the 19th century was a milestone in the newly developing science of ecology. His careful field work and affiliation with the US Department of Agriculture led to wide acceptance of his "life zones" concept.

Merriam's study area, the San Francisco Peaks in Arizona, rise nearly 6000 feet above the pine forests of Flagstaff. Photograph courtesy of USGS.

In 1889 Merriam proposed to his superiors in the federal government that he be authorized to carry out an extensive biological survey of a high mountain region "where different climates and zones of animal and plant life succeed each other from base to summit." He decided San Francisco Mountain in the Arizona Territory would be an appropriate study area "because of its southern position, isolation, great altitude, and proximity to an arid desert."

Merriam and his expedition members arrived in Flagstaff on July 26, 1889. For the next two months the scientists completed extensive field work in the high forests of the peaks, out in the Painted Desert to the east, and at the Grand Canyon. The exceptional biodiversity witnessed by Merriam and his party in this relatively small geographic area led to his first publications delineating "life zones" on a regional scale.

Merriam believed that climatic gradients, especially temperature, largely determined what type of vegetative community one may find in a given location, and that these gradients were largely a function of latitude and elevation. As one moves upward in elevation temperatures decrease and precipitation increases. His regional life zones generally followed elevational belts. At 5000 feet at the northern base of the San Francisco Peaks a grassland community might be found, but just a few thousand feet higher at 7000 feet stands a ponderosa pine forest. Each of Merriam's life zones had one or more dominant species helping delineate that particular zone, e.g., ponderosa pine being the primary indicator of his "Transition" zone. Six of the zones defined by Merriam occur in relatively close proximity on the southern Colorado Plateau, from the hot depths of the lower Grand Canyon to the windswept tundra atop the San Francisco Peaks.

Merriam used his work on San Francisco Mountain to extrapolate life zones for all of North America, emphasizing that his work in Arizona was of little interest if not applied on a larger scale. He completed a map in 1893 delineating the major life zones of the continent. Although his conclusions significantly influenced early biological thought about the American west, further study has shown that there are numerous other factors affecting the distribution of biota, including aspect (i.e., which direction the slope is facing), wildfire history and frequency, and soil type. Nevetheless, modern ecologists still consider roughly Merriam's same zones the major biomes of North America.

Merriam's Life Zones 1891	***Modern Vegetation Zones***	***Elevation Range (feet)***	***Annual Precipitation***
Arctic-Alpine	***Alpine Tundra***	***11,500-12,700***	***35"-40"***
Hudsonian	***Spruce-Fir or Subalpine Conifer Forest***	***9,500-11,500***	***30"-40"***
Canadian	***Mixed Conifer Forest***	***8,000-9500***	***25"-30"***
Transition	***Ponderosa Pine Forest***	***6000-8500***	***18"-26"***
Upper Sonoran	***Pinyon-Juniper Woodland, Semi-Arid Grasslands, Semi-Arid Scrub***	***3500-6500***	***10"-20"***
Lower Sonoran	***Mojave, Sonoran, or Chihuahuan Desert***	***100-3500***	***3"-12"***

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Species Extirpations
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Succession

Changes in the Biota of the Colorado Plateau

Biota

Changes in the biota can be either natural or human-caused. Species expand and contract their ranges as a natural response to both natural climate cycles and human land use. Disturbances such as floods and fires, whatever their origins, are followed by an orderly process of recolonization known as ecological succession.

Green River, Utah. Riparian areas have seen tremendous change over the last 100 years. Photograph courtesy of Cline Library Special Collections, Northern Arizona University.

The arrival of humans on the landscape about 12,000 years ago began the era of land use as a cause of biotic change. Although the early hunters were probably not entirely to blame, the extinctions of the Colorado Plateau's megafauna were complete within 2,000 years of their arrival.

More recent changes caused either directly or indirectly by human activities on the Plateau include the extirpations of some native species, including the California condor, a number of endemic fish species, and even mammals such as the grizzly bear and the gray wolf. While the list of threatened and endangered species grows, so does the number of non-native and invasive species, especially plants such as tamarisk and Russian olive. The near extirpation of the Colorado Plateau's beaver population by early trappers began the degradation and loss of riparian areas which has become particularly serious in the last few decades. In the last 150 years, grazing, logging and fire suppression policies began to create changes in forest composition and structure which have led to the current high incidence of catastrophic wildfires. Research into the fire ecology of ponderosa pine forests has revealed that frequent low-intensity ground fires were essential to forest health.

Riparian Degradation
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Native Americans and the Environment. A comprehensive survey of twentieth century environmental issues facing Native Americans on the Colorado Plateau and throughout the Southwest, including discussions of agriculture, logging, mining, grazing, water rights, and tourism. Adapted from a published journal article by David Rich Lewis.

Late Holocene Environmental Change in the Upper Gunnison Basin, Colorado. The Upper Gunnison Basin is a high elevation (3100 to 3600 m) region on the edge of the Colorado Plateau in southwestern Colorado. Its unusual ecological characteristics include an absence of plant and animal taxa that should occur here. Fossil and archaeological evidence indicates that many of the missing species existed in the Basin during the late Pleistocene to middle Holocene. Authored by Steve Emslie.

Fire-Southern Oscillation Relations in the Southwestern United States. A close linkage between fire and climate could diminish the importance of local processes in the long-term dynamics of fire-prone ecosystems. The structure and diversity of communities regulated by fire may have nonequilibrial properties associated with variations in global climate. Successful prediction of vegetation change hinges on a better understanding of climatically driven disturbance regimes and the relative contributions of regional versus local processes to community dynamics. Adapted from a journal article by Thomas W. Swetnam and Julio L. Betancourt.

Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Where have all the grasslands gone? Numerous ecological studies across the

Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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Threatened and Endangered Species

Biota

A number of once common native plant and animal species on the Colorado Plateau have become increasingly rare, and some, particularly native freshwater fishes, have become extinct. Habitat destruction, degradation, and fragmentation, sometimes in combination with hunting and poisoning, has led to significant decreases in the overall populations of a number of species. The federal government has classified a few of these as endangered, meaning that the species is in danger of extinction throughout all or a significant portion of its range. Others, classified as threatened, may reach endangered status if habitats continue to be degraded and populations continue to fall.

For a complete list of threatened and endangered (T&E) species for Utah, Colorado, Arizona, and New Mexico click here. For a history of the California condor on the Colorado Plateau, click here. Below are brief descriptions and status of three T&E species on the Colorado Plateau.

Mexican Spotted Owl

Mexican Spotted Owl pair. Photograph courtesy of Dr. David Willey

Falling populations of the Mexican spotted owl (*Strix occidentalis lucida*) have been linked to the destruction of much of its preferred habitat. The owl uses late seral ("old-growth") forests and rocky canyonlands for nesting, roosting, and hunting prey (mostly small mammals). Harvest of old-growth timber stands, even-aged timber harvest systems, and catastrophic crown fires have contributed to loss of habitat.

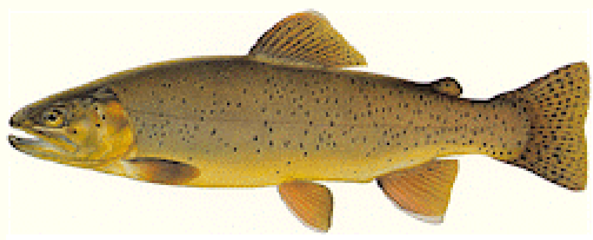
The range of the Mexican spotted owl extends to western Texas and into the mountains of northern and central Mexico. On the Colorado Plateau most of the birds occur in steep canyons ranging from central Utah and southwestern Colorado south into New Mexico and Arizona. The US Fish and Wildlife Service estimates the total U.S. population at approximately 2,700 owls.

In March 1993, the United States Fish and Wildlife Service (USFWS) listed the "Mexican spotted owl" as a threatened subspecies (there are three subspecies in North America: the Mexican, California, and Northern Spotted Owls). In 1995,

Agents of Biotic Change

the USFWS published the "Recovery Plan for Mexican Spotted Owls", which provides a long term plan to monitor the owl's progress, preserve its habitat, and ultimately, de-list the owl from the Endangered Species List. Critical habitat designation of 13 million acres across Arizona, Utah, New Mexico and Colorado was proposed in 2000.

Dr. David Willey, who has studied Mexican spotted owls in the steep canyonlands of southern Utah, found that the rocky canyon habitat provided numerous rock cavities and ledges for roost and nest sites, and provided thermal and escape cover for both the adults and young. Willey found that during winter, when ambient temperatures decrease, spotted owls were observed roosting in more open habitats, and several moved up-slope into forested highlands. This suggests that the need for thermal cover could partially explain the strong association between spotted owls and steep canyon habitat, and that these areas should be conserved while the owl is listed as threatened.



Apache Trout

Native to a small region of the southern Colorado Plateau in Arizona, Apache Trout are found only in lakes and streams of the White Mountains. The Apache trout formerly was found in the White and Black Rivers of the White Mountains, the headwaters of the Little Colorado River, and KP Creek, a tributary of the Blue River in the San Francisco River drainage. In all the fish inhabited approximately 600 river-miles. Presently, the Apache trout occupies fewer than 30 miles of small headwater streams and impoundments on the Fort Apache Indian Reservation and the Apache-Sitgreaves National Forest. The Apache trout was listed as endangered in 1969 under the precursor to the Endangered Species Act and then down-listed to threatened in 1974. The Apache trout is one of only two trout native to Arizona. This yellowish-gold fish can grow to be from 6 to 24 inches in length and weigh from 6 ounces to almost 6 pounds. They feed on aquatic and terrestrial insects.

The Apache trout is currently listed by the federal government as a threatened species as its population has dwindled. Its habitat, montane riparian areas, have been highly degraded in many areas of its range due to intensive grazing of livestock and timber-cutting operations. The Arizona Game and Fish Department is increasing its efforts in stocking Apache trout in upland streams, but without habitat restoration efforts the population will likely remain precarious.

Southwestern Willow Flycatcher

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) has declined during the last 100 years, primarily due to the loss, fragmentation, and modification of riparian habitats. Based on recent surveys coordinated by various state and federal agencies, fewer than 500 breeding pairs of the Southwestern Willow Flycatcher remain throughout its range. Surveys have also shown that the breeding sites are widely scattered and isolated, and most sites include fewer than five breeding pairs.

The breeding range includes southern California (from the Santa Ynez River south), Arizona, New Mexico, extreme southern portions of Nevada and Utah, extreme southwest Colorado, and western Texas. Another subspecies which is not endangered, *E.t. adastus*, breeds from Colorado west of the plains, to the west through the intermountain/Great Basin states, and into the eastern portions of California, Washington, and Oregon. On the Colorado Plateau, *e.t. extimus* has been detected in very small numbers along the San Juan River in southern Utah, and one or two pairs may nest along the Colorado River in Grand Canyon. They were common further upstream in Glen Canyon before the canyon was flooded to become Lake Powell after the completion of Glen Canyon Dam in 1963.

In 1993, the U.S. Fish and Wildlife Service formally proposed to list the flycatcher as a federal endangered species, and to designate critical habitat. In a 1995 ruling, the Service found that the flycatcher population was currently very low and faced a significant threat of extinction unless protected.

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The California Condor on the Colorado Plateau

Biota

California condor. Photo by Neil Johnson, Los Angeles Zoo, courtesy of State of California.

The California Condor (*Gymnogyps californianus*) is one of the world's rarest and most imperiled vertebrates. It was federally listed as an endangered species on March 11, 1967. The condor is a member of the family Cathartidae, the New World vultures, a family of seven species, including the closely related Andean condor (*Vultur gryphus*) and the sympatric turkey vulture (*Cathartes aura*). California condors are among the largest flying birds in the world. Adults weigh approximately 10 kilograms (22 pounds) and have a wing span up to 2.9 meters (9 ½ feet).

California Condors returned to the Colorado Plateau after at least a 72-year absence in December 1996 with the release of 6 birds at the Vermilion Cliffs on the Paria Plateau in northern Arizona. Of the 35 condors so far released in Arizona, 14 have fallen prey to eagles, coyotes, power lines, and, in one case, a man with a shotgun. Tragedy struck hard in the spring of 2000 when 5 mature birds died of lead poisoning, probably from eating carrion contaminated with shotgun pellets. All the Arizona condors were brought in for testing, and at this writing (summer of 2000) most are being treated for lead poisoning ranging from mild to life-threatening.

The fossil record of the genus *Gymnogyps* dates back about 100,000 years to the Middle Pleistocene epoch. The record reveals that the species once ranged over much of the southern United States. California condors nested in west Texas, Arizona, and New Mexico during the Late Pleistocene. Many fossils, eggshells, non-fossilized bones, and feathers have been found in caves within the Grand Canyon, indicating that it was an important historical nesting area. The Arizona specimens are between 9,580-22,110 years B.P., based on radiocarbon dating.

The disappearance of the condor and other large scavenging birds from these regions coincided with the extinction of the Pleistocene mammalian megafauna,

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their primary food source. By the time European man arrived in western North America, California condors occurred only in a narrow Pacific coastal strip from British Columbia, Canada, to Baja California Norte, Mexico. There is evidence indicating that condors returned to the southwest as early as the 1700s in response to the introduction of large herds of cattle, horses, and sheep that replaced the extinct Pleistocene megafauna as a source of carrion. The last sighting of a wild condor in Arizona was in Williams, south of the Grand Canyon, in 1924.

During the early 1900s condors were threatened by predator-poisoning campaigns, egg collecting, and museum collecting. More recently lead poisoning, collision with wires, and shooting have been the main causes of the population decline. By 1982 only 22 condors existed in the world. It was decided that the only way to prevent extinction of the species was to capture the last wild birds for captive breeding, with the intention of later reintroducing the offspring into the wild. On 19 April 1987, the last wild California condor was taken into captivity.

The recovery plan for the California Condor called for the maintenance of at least two non-captive populations and one captive population. These three populations must: (1) each number at least 150 individuals, (2) each contain at least 15 breeding pairs, and (3) be reproductively self-sustaining and have a positive rate of population growth. Following a widely publicized solicitation for suggestions for suitable condor release sites outside of California, the California Condor Recovery Team recommended in December 1991 that condor releases be conducted in northern Arizona. Because this area once supported California condors, and still provides a high level of remoteness, ridges and cliffs for soaring, and caves for nesting, the probability of a successful reintroduction was deemed very good.

In 1995 a release site was chosen near the edge of the Vermillion Cliffs on the southwestern corner of the Paria Plateau in northern Arizona just north of Grand Canyon. The Paria Plateau is characterized by relatively flat, undulating topography dominated by pinyon-juniper/blue grama grass communities and mixed shrub communities dominated by sagebrush on sandy upland soils. To the south and east of the Plateau lies the steep precipice of the Vermilion Cliffs, rising over 1,000 feet from the floor of House Rock Valley. Uplifting and differential erosion has created complex geologic structures and a diverse variety of habitats in a small geographic area. The cliffs are sharply dissected by canyons and arroyos and the lower slopes are littered with enormous boulders. Numerous springs emerge from the sides of the cliffs.

Whether the California Condor will survive in the wild is currently an open question. Ultimately it may be decided not only by the past land use history of the Colorado Plateau, but also by land-use decisions that we make today.

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/ Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation

Endangered Fish on the Colorado Plateau

Biota

Adapted from: Mac, M. J., Opler, P. A., Haecker, C. E. P. and Doran, P. D., editors. 1998. *Status and Trends of the Nation's Biological Resources - Southwest.* United States Geological Survey, Biological Resources Division, 986 pp. Also available at <http://biology.usgs.gov/s+t/SNT/noframe/sw152.htm>.

Introduction

Freshwater fishes are the most imperiled vertebrate group in the United States (Williams et al. 1989; Minckley and Deacon 1991; Warren and Burr 1994). In the United States, about 20% of fishes are extinct or imperiled, as compared with 7% of the country's mammals and birds (Master 1990). Almost 30% of the surface land area in the conterminous United States occurs west of the Continental Divide, but only about 21% of the roughly 800 freshwater fishes native to the United States are found there. Aquatic ecosystems in western North America, however, particularly in the Southwest, are endowed with some of the highest rates of endemism on the continent. In the Colorado River basin, for example, 35% of all native genera and 64% of the 36 fish species are endemic (Carlson and Muth 1989). The other southwestern watershed that demonstrates a high degree of fish endemism (30%) is the Rio Grande in New Mexico.

The level of threats to western fishes is also high and is probably best reflected in the number of imperiled species found in each state. Southwestern states have some of the highest percentages of threatened fish fauna: Arizona, 85%; California, 72%; New Mexico, 30%; and Utah, 42% (Warren and Burr 1994; Fig. 1).

Because we cannot present all possible situations affecting southwestern fishes, we emphasize factors relevant to the decline and demise of these fishes by using shared ecological traits to illustrate the problems faced by these fishes. Fish communities of the main-stem Colorado River and

[Loss of Beaver](#)
[Wildfire History and Ecology](#)
[Ponderosa Fire Ecology](#)
[Tamarisk Invasion](#)

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associated major tributaries, mountain headwater systems in the Gila River drainage (see box on Gila Trout), and the main-stem Rio Grande are discussed here (Fig. 2). The fishes in these communities range from long-lived, large-bodied fishes found in large, highly variable rivers to small, specialized fishes that have been isolated for thousands of years in relatively stable environments.

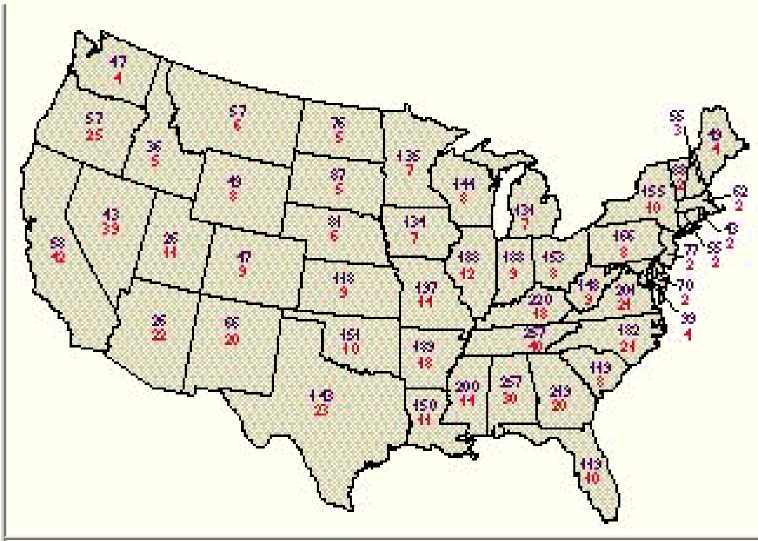

Fig. 1. Numbers of native freshwater fish species in the lower 48 states (purple number) and number of fishes recognized by fisheries professionals as endangered, threatened, or of special concern (red number; based on Warren and Burr 1994). Regionally, more than 48% of the fishes in the Southwest have been identified as jeopardized, compared with 19% in the Northwest and 10% in the Southeast (Warren and Burr 1994).

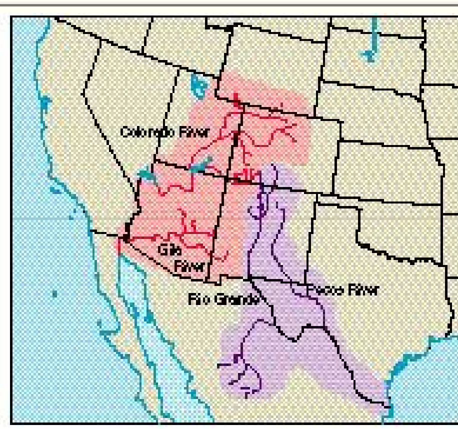

Fig. 2. Major river drainages in the Southwest.

Colorado River Fishes

Perhaps no other group of fishes better exemplifies the problems confronting aquatic ecosystems in the Southwest than the fishes of the Colorado River basin. More studies have been conducted and reports written on this group of fishes than any other assemblage of nongame fishes in the region. The Colorado River basin is the largest watershed in the Southwest, draining portions of seven western states, including about one-twelfth of the land area in the contiguous United States. The threats to this ecosystem are numerous and synergistic. Numerous dams on the main-stem river represent the most significant environmental perturbation facing these fishes. Main-stem impoundments have drastically changed water temperature, converted the river from sediment-laden to relatively clear, altered historical patterns of spring floods and the general water-flow regime, and blocked migratory pathways for fishes. Consequent modification or loss of habitat for native species and the creation of suitable habitat for nonindigenous fishes have irreversibly altered the Colorado River aquatic ecosystem.

Although only 36 native freshwater fish species formerly lived in the Colorado River basin--a low number relative to basins east of the Continental Divide--species-level endemism is high (64%) (Carlson and Muth 1989). The number of native species in the major Colorado River basin drainages ranges from 5 (Bill Williams River) to 18

(Gila River). Although many of these endemic species are restricted to specific river systems in the Colorado River (for example, Virgin spinedace--Virgin River; spikedace and loach minnow--Gila River; woundfin--Virgin, Salt, and Gila rivers), several endemic taxa once were found generally distributed in main-stem habitats throughout the basin.

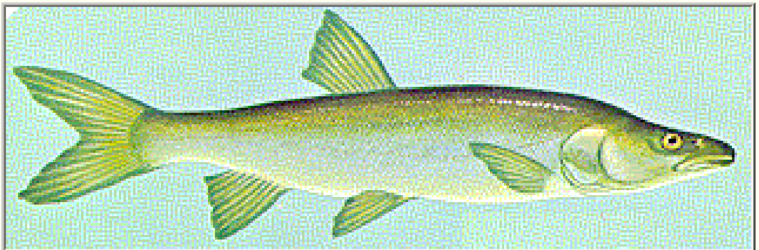

Fig. 3a. Colorado Squawfish (Ptychocheilus lucius). Anecdotal accounts refer to squawfish 2 meters long and weighing 45 kilograms. The maximum weights recorded in historical collections were 30 to 40 kilograms. Illustration by Kent Pendleton. Courtesy of Colorado Division of Wildlife. Colorado Outdoors, May-June, 1975.

Fishes that inhabit and evolved in large rivers in the Colorado River basin are members of the chub complex (roundtail chub, humpback chub, and bonytail), Colorado squawfish (Fig. 3a), and the razorback sucker. Of this group, four species are listed as endangered and one (roundtail chub) is a sensitive species (formerly Category 2 candidate; U.S. Fish and Wildlife Service 1994a). Most recent fisheries investigations have been directed at the three endangered Colorado River cyprinids--Colorado squawfish, humpback chub, and bonytail.

Studies on the Colorado squawfish (*Ptychocheilus lucius*, a.k.a. Colorado pikeminnow) demonstrated that it is a highly migratory species that formerly occurred throughout the basin but is now reduced to about one-third of its original range. Natural populations of this large-river fish have been eliminated from the lower basin, and the species is rare in the upper basin.Humpback chubs inhabit relatively inaccessible reaches of the Colorado River system. Although this endemic Colorado River fish probably was found historically in most large-river habitats of the Colorado River, it now exists in only five canyon reaches in the upper basin--in the Grand Canyon in Arizona and near the confluence of the Colorado and Little Colorado rivers. Researchers believe that this last locality harbors one of the largest remaining humpback chub populations and that it is the spawning locality of Grand Canyon populations.

Fig. 3b. Bonytail chub (Gila elegans). Historically, the bonytail was probably one of the most abundant fishes in the Colorado River basin but has now been called functionally extinct (Carlson and Muth 1989). Illustration by Kent Pendleton. Courtesy of Colorado Division of Wildlife. Colorado Outdoors, May-June, 1975.

Bonytails (*Gila elegans*, a.k.a. bonytail chubs; Fig. 3b) are the rarest of the endemic big-river fishes of the Colorado River. This fish species experienced the most abrupt decline of any of the long-lived fishes native to the main-stems of the Colorado River system and, because no young individuals have been found in recent years, has been called functionally extinct (Carlson and Muth 1989). Bonytails were one of the first fish species to reflect the changes that occurred in the Colorado River basin after the construction of Hoover Dam; the fish was extirpated from the lower basin between 1926 and 1950. In reference to the rapid demise of bonytails, Behnke and Benson (1980:20) said, "If it were not for the stark example provided by the passenger pigeon, such rapid disappearance of a species once so abundant would be almost beyond belief." Bonytails were also extirpated from several upper basin rivers (Green, Gunnison, and Yampa rivers) where they were once common. Populations in free-flowing waters now apparently survive only in the Colorado River in Colorado and Utah. The largest population of bonytails occurs in Lake Mohave (Mueller and Marsh 1995), but this population consists only of old individuals, and there is no evidence of reproduction.

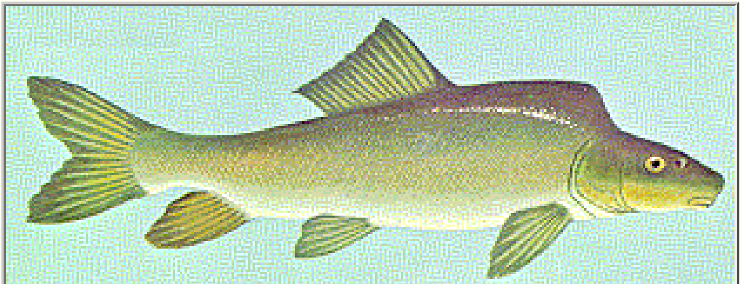

Fig. 3c. Razorback sucker (Xyrauchen texanus). A principal commerical fish in the early 1900s, this species has had no significant reproduction in recent years. Illustration by Kent Pendleton. Courtesy of Colorado Division of Wildlife. Colorado Outdoors, May-June, 1975.

Only recently have investigations begun to focus on the razorback sucker (*Xyrauchen texanus*, Fig. 3c)--one of the most threatened big-river fishes in the Colorado River basin (Mueller and Marsh 1995). This fish was formerly so abundant throughout the main-stem and major tributaries of the Colorado River basin that in the early 1900s it was one of the principal fishes taken by a commercial fishery in southern Arizona (Hubbs and Miller 1953). Additional anecdotal accounts of the abundance of razorback suckers occur in historical reports from the 1880s through the 1940s. This unique fish now inhabits only 1,208 (river) kilometers in the upper basin, while the only substantial population in the lower basin occurs in Lake Mohave (McAda and Wydoski 1980; Marsh and Minckley 1989). The most serious problem for the razorback sucker is the lack of any significant reproduction in recent years.

The dilemma of big-river fishes in the Colorado River basin is not limited to these species, which are accorded some level of federal protection. For example, the flannelmouth sucker, one of the most common suckers in many portions of the upper basin, has been eliminated from the Gila River drainage.

Concurrent with the decline in native fish species has been an increase in the species richness and abundance of nonindigenous fishes. Maddux et al. (1993) reported the introduction of at least 72 fish species, twice the number of native fishes, into the Colorado River basin. Many of these introduced fishes have established successful populations in parts of the Colorado River system and now are serious predators of young suckers, chubs, and squawfish.

Causes of Imperilment

Little debate occurs among fisheries professionals about the causes of imperilment and extinctions of southwestern fishes. Most frequently mentioned causes are construction of dams, loss of physical habitat, habitat degradation, chemical pollution, overexploitation, and introduction of nonindigenous species. Dam construction and regulation probably had the greatest adverse effect on native fishes of southwestern rivers, while the effects of excessive groundwater pumping have imperiled many spring systems and their associated fauna. The number of nonindigenous fish species in the Southwest is considerable: Arizona has 71 species; New Mexico, 75 species; Utah, 55 species; and Texas, 96 species (Boydstun et al. 1995).

As a whole, fishes in the western United States are clearly more imperiled than those in the eastern United States. More than half of the fishes listed as endangered or threatened by the U.S. Fish and Wildlife Service, or being considered for such listing, occur west of the Continental Divide. The commonly observed pattern is the disappearance of the most sensitive fishes, followed by the collapse of whole fish faunas in major western river basins. If current efforts directed at recovery of native western fishes are not continued and successful, we could witness the disappearance of most of the region's endemic fish fauna.

Recovery strategies for aquatic organisms in the Southwest vary depending on their perceived problems and life-history strategies. In general, researchers know what is required to recover most threatened and endangered fishes, but some solutions (for example, removing dams) may be unrealistic and controversial. The most frequently cited solution is habitat preservation, which may be relatively simple for fishes with restricted distributions and small population sizes. Recovery strategies for long-lived, wide-ranging species, such as the Colorado squawfish, are more complex and require a long-term commitment. The unique ecological requirements of the various life-history stages of long-lived species dictate the need for protection of extensive river reaches and perhaps changes in water use. Realistic possibilities for recovery of the native fish fauna of the Southwest are decreasing as human populations increase and formerly uninhabited lands become developed, causing native fish populations to decline further.

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Mammal Populations

Adapted from: Mac, M. J., Opler, P. A., Haecker, C. E. P. and Doran, P. D., editors. 1998. *Status and Trends of the Nation's Biological Resources - Southwest.* United States Geological Survey, Biological Resources Division, 986 pp. Also available at http://biology.usgs.gov/s+t/SNT/noframe/sw152.htm

Desert bighorn sheep (Ovis canadensis nelsoni). Photo courtesy H.E.McCutchen

Within temperate North America there are 37 families with 643 species of mammals. The Southwest contributes impressively to this diversity; native mammal species in southwestern states number about 120 in Texas, 138 in Arizona, 139 in New Mexico, and 163 in California (Findley et al. 1975). No other region in the country has so many mammal species–and many of these species and their named subspecies are endemic to the Southwest.

On the Colorado Plateau changes in native mammalian diversity began to be apparent by the late 1800s and early 1900s with the arrival of the railroad and the large numbers of livestock it brought to the region. With the decline of native ungulate populations (Mackie et al.1982) during and following Anglo settlement, large native carnivores such as grizzly bears, gray wolves and mountain lions began to prey on domestic livestock. The Bureau of Biological Survey trapped huge numbers of predators, eventually extirpating the gray wolf and grizzly bear from the region (Brown 1983). An effort is now underway to reintroduce the gray wolf in a few unsettled areas.

The activities of the black-tailed prairie dog–grazing and construction of burrows and mounds–and, by association its chief predator, the black-footed ferret, put these two species in conflict with farmers and ranchers as well. Eradication campaigns, primarily using poison, reduced prairie dog distribution from 40,000,000 hectares to 600,000 hectares by 1960–about a 98% decline in the original geographic distribution of the species (Miller et al. 1990). The black-footed ferret nearly became extinct, and efforts are now underway to reintroduce the species into some prairie dog colonies.

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Black-footed ferret (Mustela nigripes)

20th-century management of deer and elk populations for game hunting and continued trapping of carnivores (including mountain lions) in the Southwest and have resulted in recovery of ungulates from turn-of-the-century population lows (Mackie et al.1982). Although elk were extirpated from the region, they were reintroduced by state game departments (and other game agencies) from areas to the north, such as Yellowstone National Park (Findley et al. 1975; Hoffmeister 1986). Elk numbers are now at an all-time high, and once again causing conflicts with livestock ranchers. In many areas, mule deer and white-tailed deer also have made remarkable recoveries from earlier lows, although in some areas nonindigenous deer have been transplanted (Hoffmeister 1986).

Other ungulate populations have remained at low levels. Despite considerable transplant efforts, desert bighorn sheep may only be at 2%-8% of their population levels at the time of Anglo settlement. These animals have never recovered from unregulated harvesting, habitat destruction, overgrazing of rangelands, and diseases contracted from domestic livestock (Singer 1995). Numbers of Sonoran pronghorn, listed as endangered by the U.S. Fish and Wildlife Service, are also low and continuing to decline on the Colorado Plateau.

Only recently has concern been focused on other less conspicuous mammals that differ in habits from those that were in conflict with humans during settlement. The last list of candidate and sensitive species (U.S. Fish and Wildlife Service 1994) includes a broad spectrum of mammals that are of concern. The list no longer emphasizes large carnivores, or many carnivores at all, but instead emphasizes smaller species such as insectivores (shrews), a wide array of bats, cottontails and hares, pocket gophers, tree squirrels, and a variety of mice and rats. In general, we know little of the status and trends of these species.

Several unifying trends exist among mammals on these lists, excluding bats (U.S. Fish and Wildlife Service 1994). Many of the mammals, including shrews, gophers, tree squirrels, mice, and rats, have small or restricted ranges, often on single mountaintops or other functional islands. Many mammals on the lists are isolated subspecies of wide-ranging species and often occur on different mountain ranges (Hall 1981). Also, and perhaps more importantly from an ecosystem perspective, many of the species or subspecies live in wet or moist habitats, often montane. This is clearly the case for the shrews, voles, meadow jumping mice–a unique family of mice found in North America and China–and some other mice.

A smaller number of mammals adapted to arid habitats (for example, kangaroo rats, pocket mice, and cotton rats), primarily in Arizona and Utah, are also on the sensitive species list (U.S. Fish and Wildlife Service 1994). Possible environmental threats to pocket gophers include habitat change through overgrazing, lowering of water tables, and poisoning campaigns directed against them or other rodents, such as prairie dogs. Gophers, like prairie dogs, perform ecologically important roles through their habit of turning over and aerating soils, thereby providing for percolation of water and creation of new substrates for vegetative succession.

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Pleistocene Megafauna Extinctions

Biota

Source: Stevens, William K. 1997. New Suspect in Ancient Extinctions of the Pleistocene Megafauna: Disease. *New York Times*, 4-29-97.

When the first humans migrated from Asia to North America 15,000 years ago or more, they confronted an array of big animals more dazzling than that of modern Africa. Mammoths, mastodons, camels, horses and a stately deer called the stag-moose coexisted with giant ground sloths and beavers the size of today's black bears.

These plant-eaters were prey for meat-eaters like saber-toothed cats, savage short-faced bears, cheetahs, maned lions and dire wolves, bigger versions of today's wolves. Scores of other large species roamed the continent as well.

They all vanished about 13,000 years ago in a geological eye blink of perhaps 400 years. The cause of this mass extinction and similar ones elsewhere in the world near the end of the Pleistocene era has been a much debated mystery.

One camp in the debate contends that a rapidly changing climate at the end of the last ice age did in the Pleistocene megafauna, as they are called, by transforming their habitat. An opposing camp, pointing out that the extinctions closely followed the animals' first contact with modern humans, holds that the megafauna were essentially hunted to extinction. The hunters' blitzkrieg was made easy, they contend, because the naive victims had no fear of people and were easy prey for prehistoric humans with well-honed spears.

Neither camp is about to give in, and now a third hypothesis has emerged. Scientists who find neither the climatic nor the blitzkrieg theory convincing argue that rampant disease was the main villain. In this view, the megafauna were betrayed not by the naivete of the big animals themselves but that of their immune systems. And it was not the spears carried by people that wiped them out, but the pathogens carried by dogs, rats, birds, parasites and other living baggage that accompanied the continent's first human arrivals from Siberia.

It is simply too much to believe that "a few thousand Indian men with pointed sticks could run around a continent and bring to extinction 135 species in maybe 400 years," said Dr. Ross D.E. MacPhee, a mammalogist at the American Museum of Natural History in New York, who advances the new disease

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hypothesis. He described it recently at a symposium sponsored by the museum's Center for Biodiversity and Conservation.

MacPhee is the first to acknowledge that he has an uphill battle in getting his view accepted, not least because he is only beginning to search for hard evidence to support it, and because most experts at the symposium appeared to favor the blitzkrieg hypothesis. But the originator and chief advocate of that view, Dr. Paul S. Martin of the University of Arizona, said he wished he could accept the disease hypothesis, even though he considered it improbable. It would add another mechanism, in addition to hunting, by which humans could have instigated the extinction of so many species.

Others welcomed the new entry in the debate, even though they remained skeptical. "It's wonderful that it's being thrown into the mix," said a blitzkrieg supporter, Dr. Tim F. Flannery, a research scientist at the Australian Museum in Sydney.

There have been a number of mass extinctions in the earth's history, and scientists believe most have been caused by changing climate or the impact of asteroids or comets. The disappearance of the dinosaurs some 65 million years ago was one of those events. But the North American extinctions at the end of the ice age differed from earlier ones: they coincided not only with the most recent retreat of the great glaciers but also with the first appearance of human hunters, they were very rapid and they were severe only in big mammals; small mammal species were generally unaffected.

Those who subscribe to the climate-change theory of the extinctions argue that the driving force behind them was the destruction of habitat brought about by oscillating periods of warmth and cold during the Pleistocene era, the era of on-and-off glaciation that began about a million years ago.

In this hypothesis, advocated by Dr. Russell W. Graham of the Denver Museum of Natural History among others, North America in the earlier Pleistocene was dotted shore to shore by different habitats, each favorable to particular species. As a result, the megafauna were widely distributed as well, since they could find forage anywhere. But the changing climate, according to this hypothesis, changed the landscape as well; instead of widely scattered patches, habitat types like forest, savanna and prairie tended to be increasingly limited to certain parts of the continent. Over hundreds of thousands of years, this gradually shrank the ranges of the large animals, whose survival required not only suitable forage but also lots of territory from which to glean it. The stag-moose, for instance, became confined to the Great Lakes region.

Critics of this view argue that there was little difference between the climatic changes that occurred at the end of the last ice age and those at the end of several earlier glaciations, when the same kinds of animals did not go extinct. But Graham replies that since the geographic ranges of animals were gradually reduced over a long time, no out-of-the-ordinary climatic event was required.

The blitzkrieg theory, on the other hand, points to the remarkable coincidence of mass extinctions with the first arrival of prehistoric but anatomically modern humans in many parts of the world at various times over the last 40,000 years. Only Africa, where humans and megafauna evolved together over millions of years, is an outright exception. But in general, there was what MacPhee calls "this dreadful syncopation -- humans arrive, animals disappear."

Martin's blitzkrieg theory goes this way: The first humans to arrive in North America from Siberia were already highly skilled, experienced hunters of big game. The continent that greeted them was rich in big animals, and the package of nourishment in a single animal was so large that "you can waste it and go out and kill another one." These optimum conditions would have enabled the new human populations to expand to their maximum. The expanded populations would sweep over the landscape, flooding a given area with people for a year or two before moving on.

"The animals totally new to this kind of encounter will vanish," Martin said. The killing front would advance perhaps 100 miles in 10 years, he said, eventually resulting in a continent-wide mortality rate far above what large mammal populations can survive given their relatively slow reproduction rates and normally low death rates.

Critics of the blitzkrieg hypothesis point to a paucity of fossil evidence showing that hunters killed big game. Such evidence has been difficult to find, Martin said, partly because one must look for it in an extremely thin geological stratum representing only a decade. Even today, according to one report at the New York symposium, it is difficult if not impossible to find evidence in the remains of thousands of modern elephants, shot in Africa as part of recent efforts to cull herds, that they were killed rather than dying naturally.

In another objection, MacPhee points out that hunters of the 19th and 20th centuries could not wipe out the great whales (blitzkriegers say the ocean is very large) or the American bison. Blitzkriegers reply that not all big mammals would necessarily have been killed by Pleistocene hunters, and indeed bison, deer, elk, moose, wolves and mountain lions are among the survivors. Moreover, they say, the bison and some others have been saved only through present-day conservation efforts.

Nevertheless, MacPhee says he still disbelieves the idea that primitive people could wipe out a whole continent full of mammals amounting to more than 11 dozen species. "You would have to do nothing morning, noon and night except kill," he said, "and kill on a scale never seen in any technologically sophisticated society."

The disease hypothesis, worked out by Dr. MacPhee and Dr. Preston A. Marx, a virologist at the Aaron Diamond AIDS Research Center in New York, holds that the animals were infected by lethal pathogens unknown to their immune systems. (Similarly, diseases introduced later by Europeans ravaged populations of immunologically defenseless Indians.) As envisioned by Marx, disease would have advanced across the continent in the wake of humans, either reducing animal populations to levels from which they could not recover or springing up again and again to infect new generations.

For this to have happened, Marx said, several conditions would have been necessary: The killer pathogen would have had to kill rapidly. It would have had to affect all age groups in a given animal population (something hunters do not do). It would have had to have an independent host, either people or creatures that arrived with people, to provide a reservoir of immune carriers from which the disease could spread. And it would have had to affect a broad array of species without causing epidemics in humans.

A number of diseases meet some of the criteria; canine distemper and rinderpest, for instance, have all caused severe reductions in populations of several animals. But they have not caused any known extinctions. MacPhee and Marx have so far identified only two existing pathogens that fulfill all the requirements: leptospirosis, a bacterium spread in rat urine, and the rabies virus. The point is not that either of these diseases were necessarily the actual agents of extinction, the two scientists say, but rather that there exist some pathogens that conceivably could have done the job.

The disease hypothesis can be tested, MacPhee said, by examining mummified remains of Pleistocene animals to see if there are genetic traces of disease organisms in their bodies. He and Marx are setting out to perform such tests. "Our assumption is that the pathogen is still with us in a more benign state and that existing species are handling it well enough to survive," Marx said. That would provide some clue as to what to look for. But if the responsible pathogen is itself extinct and has no present-day relatives, he said, "we're going to have a tough time finding it."

Could the extinctions have had multiple causes? One expert, Dr. A.J. Stuart of the Norfolk Museums Service in Norwich, England, argues that climatic change did indeed reduce some populations of Eurasian megafauna to vulnerable levels, and that hunting pressure supplied the coup de grace. One set of extinctions took place roughly coincident with the arrival of modern humans in Europe about 40,000 years ago, but others did not take place until later. While these later extinctions did not coincide with the first arrival of humans, they did coincide with the climatic disruptions that occurred at the end of the ice age. Stuart calls this "a potent reason" for rejecting the idea that human overkill alone caused the extinctions.

Another possible factor is that big carnivores shifted their attention to more kinds of animals as humans killed their preferred prey, thereby helping to press the substitutes to extinction. Once their prey became extinct for whatever reason, it is widely thought, many of the predator species vanished as well. In any case, the American maned lion, the dire wolf, the short-faced bear and the saber-toothed cat no longer exist.

Some scientists see the idea of multiple causes as a kind of intellectual cop-out. It is better, said MacPhee, for one, to "develop and test hypotheses singly and then they either succeed or fail singly."

But the day when that happens, or when it becomes clear that several causes are responsible, appears far off.

by William K. Stevens **© New York Times, 4-29-97.**

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology
Ponderosa Fire Ecology

Exotic and Invasive Species

Biota

Dalmation toadflax (Linaria dalmatica). Photo courtesy of Chris Luginbuhl

Invasive plant and animal species–also referred to as exotics, non-natives, introduced, or nonindigenous species–are organisms which have expanded beyond their native range or have been introduced from other parts of the world. Some species were introduced into the wild intentionally, while others have been introduced unintentionally and expanded on their own.

Of particular concern on the Colorado Plateau are introduced weedy plants which are invading rangelands, forests, and riparian ecosystems at an alarming rate. Human activities such as grazing of livestock or logging, with its associated road networks, often disturb biotic communities enough to allow establishment and in some cases domination of invasive species. Control of infestations has been difficult, and the ecological consequences have been serious. Negative impacts include reduction in biodiversity, forage, habitat and aesthetic quality, and even soil productivity. The rapid expansion of exotic weed populations has been a deterrent to restoring native plant communities and re-establishing historic ecological conditions.

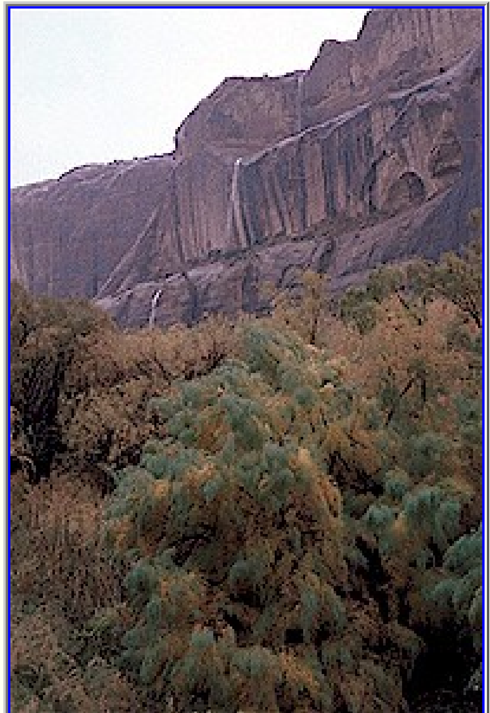
Saltcedar or Tamarisk

One of the most important, and damaging, introduced species on the Colorado Plateau is saltcedar, or tamarisk. Eight species of this small riparian tree were purposely introduced in the western United States as ornamentals, for windbreaks, or to help control streambank erosion. Some of these species, principally *Tamarix ramosissima*, but also *T. chinensis* and *T. parviflora*, have established themselves in nearly every lower-elevation streambed from northern Mexico to southern Canada and now cover approximately 1.5 million acres.

Tamarisk Invasion

Agents of Biotic Change

Native riparian cottonwood/willow communities, which support some of the highest numbers of breeding bird species found in any vegetative community type in the United States, have declined dramatically as tamarisk has invaded. The plant, without any native checks, has replaced thousands of acres of riparian gallery forest, resulting in a significant decrease in biodiversity and ecosystem health along most of the Colorado Plateau's waterways. Click here for a more comprehensive essay on tamarisk by ecologist Dr. Larry Stevens.



Tamarisk thickets along the Colorado River near Moab. Photo © 1999 Ray Wheeler.

Cheatgrass

Cheatgrass (*Bromus tectorum*) is a winter annual grass which originated in Europe and Asia (Eurasia) and came to our area in contaminated seed in the 1890s. By 1920, cheatgrass, or downy brome as it also is known, had invaded native semi-arid grasslands and open pinyon-juniper woodlands of the Colorado Plateau. Despite its early growth and rich color, cheatgrass is unpalatable to sheep and other livestock, which tend to overgraze native plants when it begins to prevail.

Most native bunchgrasses of the Colorado Plateau are perennial, whereas annual plants like cheatgrass grow from a seed, then flower, set seed, and die every year. Cheatgrass usually germinates in fall and grows during winter, opposite the cycle followed by common native perennial grasses. By the time the rain stops in spring, cheatgrass already is maturing its seeds. Unlike native bunchgrasses, cheatgrass then dies by the end of July, avoiding the hottest and driest part of summer.

Dead cheatgrass burns easily, causing early and abundant wildfires which tend to damage or kill native grasses. During a fire, early-maturing cheatgrass seeds can take advantage of many nutrients the fire releases to grow large and produce abundant seed (over a thousand per plant in some cases).

Because cheatgrass quickly develops a large root system in the spring, by the time native grass seedlings start to grow in April or May, cheatgrass has stolen most water out of the top foot of soil. Although mature native grasses can get water from lower soil regions, seedlings cannot get their roots deep enough into soil to access water before drought sets in, and thus, die of thirst. Without this ability to reproduce, native grasses inevitably decline, and so over time, cheatgrass becomes more and more common until eventually it dominates. Cheatgrass often opens the way for secondary invaders such as knapweed and thistle

Other harmful introduced species found in plant communities on the Colorado Plateau include Dalmation toadflax (*Linaria dalmatica*), leafy spurge (*Euphorbia esula*), and camelthorn (*Alhagi pseudalhagi)*), which is primarily spread by livestock grazing and wind.

Southwest Exotic Plant Information Clearinghouse (SWEPIC) is a cooperative effort among the U.S. Geological Survey, the National Park Service and Northern Arizona University to organize comprehensive information on exotic plant species in the southwest on one web location. SWEPIC is to help all people and organizations committed to protecting the ecological and economic values of southwest resources from degradation from harmful non-native weeds. The goal of SWEPIC is to provide reliable and organized information on the distribution and ecology of these weeds in the southwest, with an emphasis on forests, rangelands, and other natural areas.

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Forest Composition and Structure

Lt. Edwin Beale, traversing northern Arizona on an exploratory expedition in 1857, had this to say about the forests of this region of the southern Colorado Plateau.

"We came to a glorious forest of lofty pines...The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, it was not so in this instance; every foot being covered with the finest grass, and beautiful broad grassy vales extending in every direction. The forest was perfectly open and unencumbered with brush wood, so that the travelling was excellent... "

Forest rangers marking ponderosa pine for timber sale near Flagstaff, Arizona, 1909. Image 57a by A.G. Varela courtesy of Cline Library Special Collections, Northern Arizona University.

There is ample evidence that prior to extensive Anglo settlement much of the ponderosa pine forests of the region were as characterized by Lt. Beale, open "park-like" stands of large, old ponderosa pine underlain by a rich understory of native herbs and grasses (see 1909 photo at right). Periodic small wildfires maintained this open structure by killing ponderosa seedlings and encouraging growth of grasses.

Today's ponderosa pine forests of the southern Colorado Plateau little resemble those which Lt. Beale described. The introduction of livestock grazing, logging, and fire suppression, combined with a series of wet climate pulses early in the century, have resulted in forests which are characterized by "dog-hair thickets," dense clumps of small trees competing for space and nutrients. Grasses and forbes on the forest floor have been dramatically reduced compared to pre-settlement conditions, replaced by thick accumulations of dead pine litter.

Until 20 years ago, snags (dead trees) were systematically removed as fire and forest health hazards. Those that remained were often the focus of timber poachers, aided by the extensive road networks created for legal logging operations. Most managed forests now lack desired numbers of large-diameter snags, which serve important ecological roles such as cavity-nesting sites for many breeding birds and probably for many bats as well.

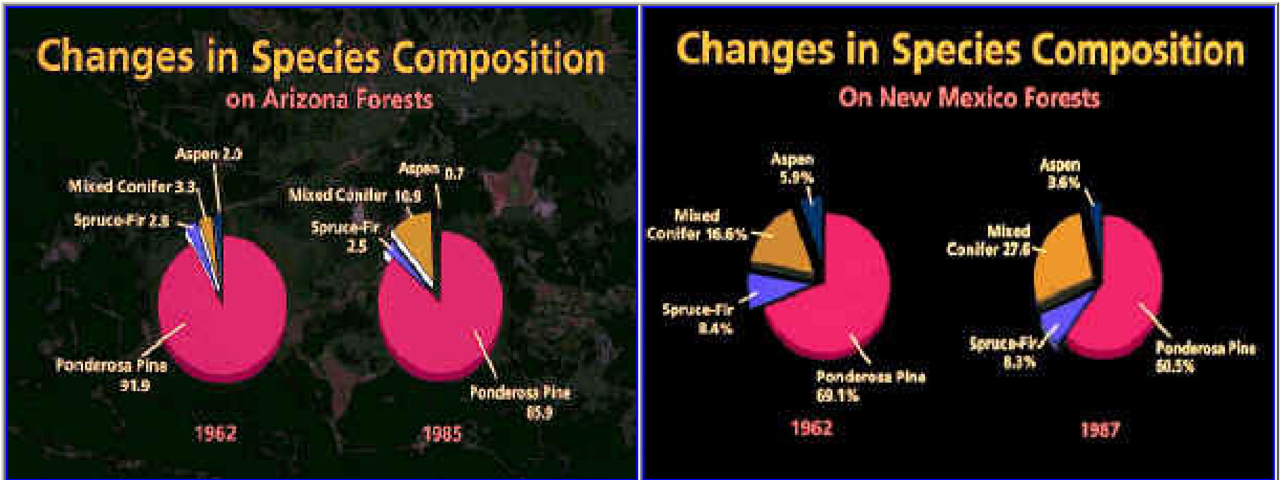
The loss of native grasses palatable to livestock may be contributing to higher elk browsing of young quaking aspen. Continuous browsing of aspen sprouts eventually results in the death of the sucker root system and the ability of aspen clonal systems to regenerate. There has been large decline in the quaking aspen cover type in just the last 30 years, representing a significant loss of biodiversity at the landscape level. This broadleaf component of mixed-conifer forests is important to many species of wildlife, particularly birds and invertebrates such as the western tiger swallowtail and red-spotted purple butterflies.

The figures below show some significant changes in the abundance of different forest types in Arizona and New Mexico over a 25-year period from 1962 to 1985. The U.S. Forest Service estimates that the extent of aspen stands in Arizona and New Mexico declined by an 46% during this time, while areas dominated by

Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of Plants
Succession
Riparian Degradation
Loss of Beaver
Wildfire History and Ecology
Ponderosa Fire Ecology
Tamarisk Invasion

Agents of Biotic Change

mixed-conifer forests increased by 81%.



Figures courtesy of Southwestern Region USFS Rocky Mountain Research Station. From General Technical Report RM-GTR-295, http://www.rms.nau.edu/publications/rm_gtr_295/

Research: Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Restoring Ecosystem Health in Ponderosa Pine Forests of the Southwest. Restoration of ecosystem structure and reintroduction of fire are necessary for restoring rates of decomposition, nutrient cycling, and net primary production to natural, presettlement levels. The rates of these processes will be higher in an ecosystem that approximates the natural structure and disturbance regime. Adapted from a 1997 journal article by W. Wallace Covington *et al*.

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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Biota

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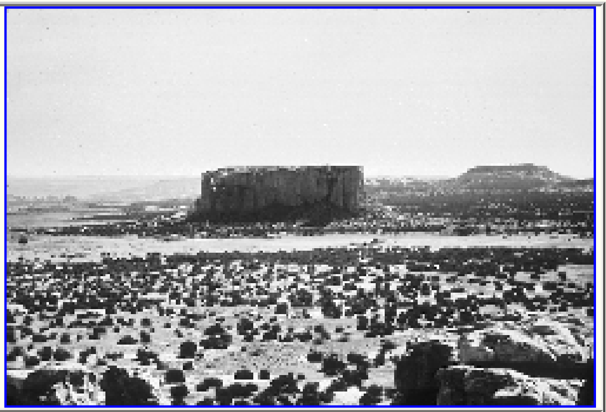
Species' Range Expansion

Biota

Species' ranges can both expand and contract over time. For example, ponderosa pine rapidly expanded onto the Colorado Plateau over thousands of years following the end of the Pleistocene. The range of the pine may have contracted locally over the last 50 years due to the ecologic effects of fire suppression.

A common instance of species expansion on the Colorado Plateau over the last century has been the advancement of non-palatable woody shrubs and trees such as sagebrush and juniper into the region's grasslands. Heavy grazing reduced community diversity and plant competition; as a result there were no fine fuels to carry surface and ground fires which were once common in the area's grasslands. Grazing also reduced competition from herbaceous species, allowed rapid growth of pinyon, juniper, oaks, and sagebrush into adjacent grassland communities (see photographs below). In the 1960s and 1970s juniper expansion blamed on fire suppression and livestock grazing justified aggressive programs of chaining and burning pinyon-juniper woodlands to improve forage and water yield.



Views from Acoma Pueblo to Enchanted Mesa, west of Albuquerque, NM, taken by William Henry Jackson in 1899 and H.E. Malde in 1977. Note expansion of junipers into surrounding grassland.
Source: C. Allen, J. Betancourt, and T. Swetnam, USGS Biological Resources Division Southwestern U.S. LUHNA pilot project, 1997 http://biology.usgs.gov/luhna/chap9.html.

Several authors have suggested that pinyon-juniper expansion may at least in part represent recovery from prehistoric fuel harvesting, at least in those areas that were heavily populated within the last 1000 years (Samuels and Betancourt 1982; Kohler 1988). Evidence also strongly suggests that there were cycles of increase and decrease in juniper woodlands during prehistoric times (Miller, 1994 p.145).

Research:

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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Land Use History of North America Colorado Plateau

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Species Extirpations

Biota

Several species native to the Colorado Plateau have been extirpated from the region over the course of this century. Many, such as the gray wolf, were actively hunted while some have been lost due to habitat degradation.

Perhaps the most widely-known or publicized species to have been extirpated from the Colorado Plateau is the grizzly bear. This large bear once roamed different parts of the Plateau, particularly the highlands rimming the area. The native Merriam's elk of the southern Colorado Plateau, a probable subspecies, was extirpated earlier this century and is now extinct. All of the Southwest's elk today are descendents of transplanted elk from the Yellowstone region of Wyoming and Montana.

Hunter with coyote pelts. Courtesy of Cline Library Special Collections, Northern Arizona University.

Federal predator control programs, formed at the request of livestock ranchers earlier this century, are largely responsible for the extirpation of both the grizzly bear and the gray wolf from the Colorado Plateau and the Southwest. Hunters were paid by the federal government to kill livestock predators, including cougars, grizzly bears, wolves, and coyotes.

A recent species reintroduction effort by the US Fish and Wildlife Service is underway in the White Mountains of Arizona that seeks to restore the previously extirpated Mexican gray wolf to a portion of its historic range.

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Status and Trends of Plants

Biota

East Tavaputs Plateau, Utah. Photo © Ray Wheeler.

The states of New Mexico and Arizona may have the greatest diversity of vascular plant species in the continental United States. New Mexico is estimated to have about 3,900 and Arizona about 3,370 species of flowering plants and ferns. Endemism is high among plants on the Colorado Plateau in Utah, but less high in more southern areas: about 5% of Arizona plant species are endemic (46 species on the Colorado Plateau), and less than 4% in New Mexico (24 are cacti, mostly in the desert regions). The number of nonindigenous or introduced species is also high; Utah has at least 580 introduced species sharing space with about 2,500 species of indigenous vascular plants.

The Plateau has some of the highest proportions of globally rare native plants in the country, about 15% of the total taxa, yet northern portions of the Plateau are some of the mostly poorly studied areas for vascular plants. The moss flora of the region, for example, is one of the least known in the United States, and our knowledge of liverworts and hornworts in New Mexico, Arizona and surrounding regions is the poorest in the country.

The list of threatened and endangered plants on the Colorado Plateau is large. Arizona, New Mexico and Utah each list from 50 to 140 taxa of plants as sensitive. These include cacti, wild buckwheats, prickly poppies, mil-vetches, paintbrushes, penstemons, sagebrushes, and others. The sunflower, pea, cactus and figwort families account for more than half of the species of special concern in New Mexico. For a list of threatened and endangered species on the Colorado Plateau, click here.

Land uses which have contributed to the threats to sensitive plants include grazing, fire suppression, road building, urbanization, and water diversion and development. Some cacti and plants with showy flowers have been threatened by overcollecting for the horticultural trade. As knowledge about the use of medicinal herbs by Native

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Americans has spread, populations of some of these plants have also suffered from overcollecting and poaching on public lands.

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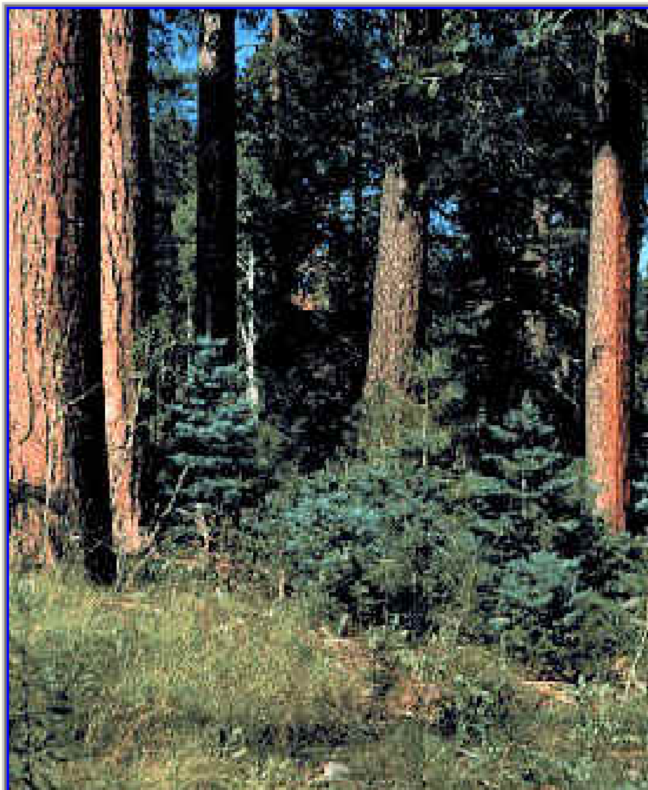
Succession

Biota



Late successional white fir beneath ponderosa pine trees. Photo courtesy of Rocky Mountain Research Station, Flagstaff, AZ.

A naturally occurring agent of change in the biotic communities of the Colorado Plateau is ecological succession. Following any disturbance, either natural or human-caused, communities undergo a somewhat orderly process of recolonization termed succession. Disturbances can include avalanches, wildfires, blowdowns, insect infestations, disease outbreaks, grazing, and logging.

Ecologists have traditionally defined plant communities based on climax vegetation. The climax vegetation of an area is that which will outcompete other species over time and eventually dominate a site for a prolonged period, perhaps several hundred years or more, *barring any new disturbance*. Communities that are considered disclimax are thought to be recently disturbed and may include several species which, though they may be abundant at this time, will eventually be excluded as the climax species takes over the site.

Succession that occurs in an area that was previously vegetated is termed *secondary* succession. This differs from *primary* succession, when species colonize a site that was previously unvegetated, such as a talus slope, a recent mudslide, or a recent glacial moraine.

Plants that initially invade sites are considered pioneer species. These species recolonize the area and essentially prepare it for the invasion of later successional species. These later seral species may occupy the site for several hundred years until finally the climax species take over.

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In forested communities, most climax tree species are tolerant of shade and establish themselves in the understory of an early seral stand. They eventually crowd out the less shade-tolerant seral species, forming a new climax forest. The photograph above shows white fir, a climax tree in some areas currently dominated by ponderosa pine, establishing new seedlings beneath the seral pine. Eventually these fir may take over this site.

Some seral species, such as ponderosa pine, are long-lived and can attain great heights. This allows them to remain part of a climax forest for an extended period of time, despite their intolerance of shade. They simply grow above the cover of the climax species and thus receive enough sunlight to sustain themselves.

Research:

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

The Social and Ecological Consequences of Early Cattle Ranching in the Little Colorado River Basin. Examines the early development of cattle ranching in the Little Colorado River Basin, the various factors which contributed to overgrazing in the region, and the pervasive effects that early commercial cattle ranching had on the local environment. Adapted from a published journal article by William S. Abruzzi.

Fire-Southern Oscillation Relations in the Southwestern United States. A close linkage between fire and climate could diminish the importance of local processes in the long-term dynamics of fire-prone ecosystems. The structure and diversity of communities regulated by fire may have nonequilibrial properties associated with variations in global climate. Successful prediction of vegetation change hinges on a better understanding of climatically driven disturbance regimes and the relative contributions of regional versus local processes to community dynamics. Adapted from a journal article by Thomas W. Swetnam and Julio L. Betancourt.

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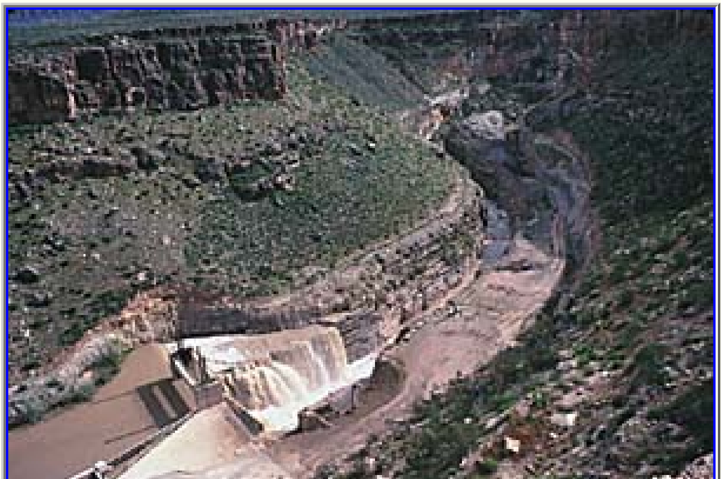
Riparian Area Loss and Degradation

Riparian areas are critical ecosystems in the semi-arid landscape of the Colorado Plateau, yet in the last few decades many have been seriously degraded and others entirely lost due to human activities and land use. Overall, a 90% loss of presettlement riparian ecosystems has occurred in Arizona and New Mexico.

The degradation of riparian communities on the Colorado Plateau began in the early 19th century with the near extirpation of the region's beaver population by fur trappers. Beavers play an important role in creating and maintaining riparian areas by cutting trees and building dams. Water retained in beaver ponds during periods of low flow support native fish populations and provide drinking water essential not only for mammal populations, but for some species of birds and bats. The trapping of alluvial sediments by beaver ponds provide opportunities for new plant growth.



A dam on the Virgin River downstream of Zion National Park. Photo © Ray Wheeler.

By contrast, human diversion or impoundment of free-flowing water by dams, diversions, irrigation, or channelization has been a major factor in the degradation of the natural functions of riparian areas. Without natural hydrologic systems, water tables have lowered, and surface sediments have dried out. Cottonwoods are particulary susceptible to water stress and may decline as groundwater becomes less available.

With less flooding, there is less channel shifting and less suitable habitat for establishment of cottonwood and willow seedlings, which are dependent on recently inundated sediments to become established. Diverse mosaics of riparian vegetation created by shifting of river channels have decreased or been eliminated in many riparian systems on the Colorado Plateau. Where existing riparian forests have aged without replacement, they have become a monoculture of maturing trees that eventually senesce, die, or become victims of fires.

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Tamarisk Invasion

Agents of Biotic Change

Overgrazing by domestic livestock has been a major factor in the alteration and degradation of riparian areas. Heavy grazing, whether by big game or livestock, deteriorates stabilizing vegetation, erodes banks, and causes declines in water storage capacity and quality. In some cases gullying or arroyo cutting occur. In others, stream beds become wider and streambeds shallower, water temperatures rise, and fish and aquatic invertebrate habitat quality declines.

Riparian systems at lower elevations on the Colorado Plateau are now increasingly characterized by a reduction of plant species diversity and density. Overgrazing of palatable native species such as willows and cottonwood saplings, combined with the introduction of less palatable nonindigenous species such as Russian olive and tamarisk, has also contributed to changes in overall plant community structure. Tamarisk, introduced to the Colorado Plateau in the 1950s, has been particularly devastating, outcompeting cottonwood and willow, and dominating lower elevation riparian systems throughout the region. Its establishment introduces a regime of episodic fire, which researchers believe is uncommon in most native riparian woodlands.

Road building, logging, construction and other development has caused additional degradation of riparian areas, especially through bank erosion. Additional nutrients and fertilizers added to stream systems by agricultural runoff and sewage treatment facilities have resulted in reductions in water quality and increased eutrophication.

As natural riparian zones are being lost, so are their associated faunas. The highest percentages of threatened fish in the United States are found in the Colorado Plateau states and California. Although only 36 native freshwater fish species formerly lived in the Colorado River basin, the largest watershed in the Southwest, species-level endemism is high at 64%. The number of nonindigenous fishes introduced into the Colorado River basin is 72, twice the number of native fishes. Four of the five fishes that evolved in large rivers in the Colorado River basin are listed as endangered, and the fifth is listed as a sensitive species. The few remaining fish stocks native to smaller riparian systems on the Colorado Plateau survive only in those areas with intact riparian habitats, often in remote upper-elevation watersheds.

The responses of riparian bird communities to changes due to grazing have been particularly well studied. At some sites 40% of riparian bird species were negatively affected by livestock grazing, and a negative correlation between recent cattle grazing and abundance of several riparian birds was found.

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Status and Trends of Plants
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Loss of Beaver
Wildfire History and Ecology

Early Fur-Trapping and the Fate of the Beaver

Biota

Adapted from: McNamee, Gregory. 1994. *Gila: The Life and Death of an American River*. Orion Books, New York.

At the time of European arrival in North America scientists estimate there may have been up to 400 million beaver living on the continent; by 1850 the number stood at only 9 million. Having eliminated the beaver from Europe by 1600, European explorers found in America a rich resource and within 250 years the pattern of extirpation had nearly been repeated. More than any other economic activity, the fur trade opened the West to American expansion. Trappers led the way for many settlers, and their names, including those of Bill Williams, Antoine Leroux, and Kit Carson, are engraved in the region's history

Line drawing courtesy of the US Fish and Wildlife Service.

The demise of the beaver brought about a major alteration of the Western landscape. The beaver is an integral part of riparian ecosystems, felling trees to create reservoirs where it builds its underwater lodges, thereby trapping alluvial sediments, providing opportunities for new plant growth, and increasing the diversity of wildlife habitats. Beaver dams help control seasonal flooding, a common occurrence on many Southwestern rivers and streams, thereby preventing erosion and downcutting of riparian channels. The reservoirs formed by dams also provide wetlands for migratory birds. Eventually these dams may be abandoned, and when they slowly break away and the pools dry up, great meadows of tall grass often grow up along the floodplain. These meadows sustain large populations of deer and elk, while the remnants of felled trees provide shelter for nesting birds and smaller animals.

The wholesale destruction of the beaver in the intermountain West disrupted these ecological relationships, and as a result erosion became a serious problem while the loss of habitat led to declining ungulate and bird populations. Removal of beavers or their dams, together with livestock grazing, has contributed to arroyo cutting and gullying of the landscape. As the channel cuts deeper and the gradient increases, the water table is lowered and surface sediments begin to dry out; gradually, the vegetation becomes composed of plants tolerant of drier conditions.

Ponderosa Fire Ecology
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Land Use History of North America Colorado Plateau

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Wildfire History and Ecology

Biota

Needle-fire in ponderosa pine. Photograph courtesy of Rocky Mountain Research Station, Flagstaff, Arizona.

Whether lightning-caused or started by native peoples, wildfires were once common occurences throughout the grasslands and forests of the Colorado Plateau. Frequent fires maintened an open forest structure in the region's middle-elevation forests, prevented tree encroachment into mountain meadows and grasslands, and in some areas replaced forested land with grassland or savannah.

Prior to white settlement, fires likely burned through the Plateau's extensive pinyon-juniper woodlands every 10–30 years, through the region's ponderosa pine communities every 2–10 years, and through mixed-conifer forests every 5–25 years. The much wetter and cooler spruce-fir forests atop the highest mountains and plateaus of the region probably went 150 years or more between fires.

The historic fire regimes changed dramatically with the arrival and settlement of Anglo-Americans. Livestock grazing removed much of the grassy fuels that carried frequent, surface fires; roads and trails broke up the continuity of forest fuels and further contributed to reductions in fire frequency and size. Because settlers saw fire as a threat, they actively suppressed it whenever they could. Initially, fire suppression was very successful because of low fuel loadings; but without fires to consume them, large fuel loads have accumulated over time.

The continuing threat of fire led to an approximately 60-year history of fire suppression policies by the United States Forest Service and other land management agencies. These efforts have resulted in far less frequent fires, disrupting the natural cycles of the region's forests and resulting in many damaging ecological effects. Forests with historically frequent, low-intensity fires were those initially most affected. Pinyon-juniper woodlands, ponderosa pine forests, and drier mixed conifer forests shifted from a fire regime of frequent, surface fires to one of stand-replacing, high-intensity fires.

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Fire suppression has contributed to the buildup of organic materials (fuels) on the forest floor. Logging has added heavy fuels in the form of limbs, tree tops, and cull logs. In some areas, these heavy fuels have been removed by slash disposal (fuel treatment), prescribed fire, or firewood collection.

By the early 1900s, fire exclusion began altering forest composition and structure. The disruption of natural fire regimes has decreased the diversity of forested areas across the landscape. Frequent fires once killed conifer seedlings encroaching into forest meadows, maintaining numerous open parks in the region's highlands. Fire exclusion permits this encroachment, and meadow acreage has decreased significantly. Establishment of young trees in older stands has provided a fuel ladder for carrying fires into the canopy. With more stand-replacing fires, average stand age is reduced; the diversity inherent in old stands is lost.

Because of heavy fuel accumulations, fires that occur now are more intense and more difficult to contain. Certainly there are more larger fires and more catastrophic crown fires today than historically. On Southwestern forests, the number of fires burning more than 10 acres has increased each decade since the 1930s. The average size of fires since the 1970s has ranged from 14 to 16 acres per fire, double the average size of fires in the earlier decades of the 1940s to 1960s.

Follow these links to:
Ponderosa Pine Fire Ecology
Reintroduction of Fire to Forest Ecosystems

Research:

Fire-Southern Oscillation relations in the Southwestern United States. A close linkage between fire and climate could diminish the importance of local processes in the long-term dynamics of fire-prone ecosystems. The structure and diversity of communities regulated by fire may have nonequilibrial properties associated with variations in global climate. Successful prediction of vegetation change hinges on a better understanding of climatically driven disturbance regimes and the relative contributions of regional versus local processes to community dynamics.

Changed Southwestern Forests: Resource effects and management remedies. Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

Where have all the grasslands gone? Numerous ecological studies across the Southwest have documented the decline in herbaceous vegetation (grasses and non-woody flowering plants) while forests thicken and brush invades. Documenting the changes in the Jemez Mountains of northern New Mexico, ecologist Craig Allen considers the evidence that these patterns are tied to changes in land use history, primarily livestock grazing and fire suppression.

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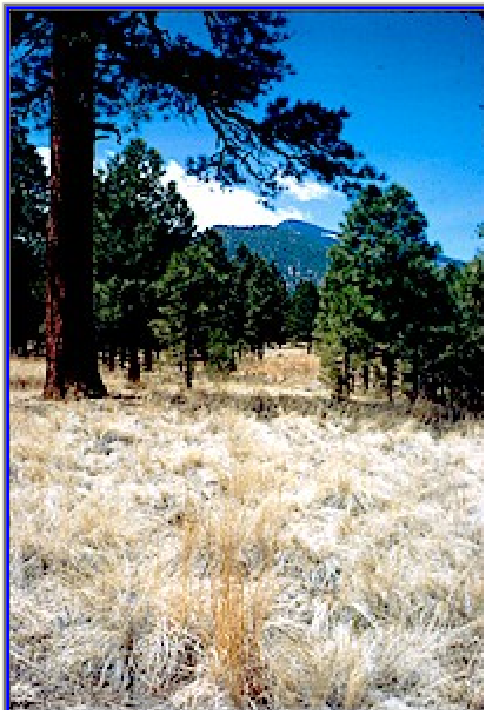
Ponderosa Pine Fire Ecology

Author: Will Moir, USFS Rocky Mountain Research Station, Flagstaff, Arizona.



Unburned grasses in ponderosa pine forest. Photo by Will Moir.

The ponderosa pine forests of the Colorado Plateau have evolved over thousands of years. Over this time the tree has developed several adaptations which help it survive in its dry, often warm habitat. A once common occurrence in these forests which has shaped the pine's particular ecological adaptations is wildfire. Recent studies indicate that the ponderosa pine forests on the southern plateau near Flagstaff, Arizona and along the Mogollon Rim were subjected to low-intensity ground fires perhaps every 2-12 years over historical time. However, beginning in the early 1900s this pattern of fire drastically changed. A fire suppression policy implemented by the United States Forest Service and other land management agencies at this time greatly decreased the occurrence of fire in these forests. The absence of reoccurring fire, coupled with widespread logging and grazing of forest lands, has led to unforeseen changes in forest composition, structure and ecology.

Today's forest is often characterized by dense "dog-hair" thickets of young pines with a thick accumulation of litter on the forest floor. Previously, many pine forests of the region were open stands of large, old ponderosa pine underlain by an understory of native grasses. Small fires maintained this open structure by killing seedlings and encouraging growth of grasses. Some ecologists recognized this change in the nature of these pine forests as a possible problem as early as the 1930s, but changes in forest management did not occur until the 1970s. Fires in many of today's ponderosa pine forests are no longer low-intensity ground fires but rather catastrophic, stand-replacing crown fires.

From about 1910 to approximately 1990, the amount of acres burned by wildfire

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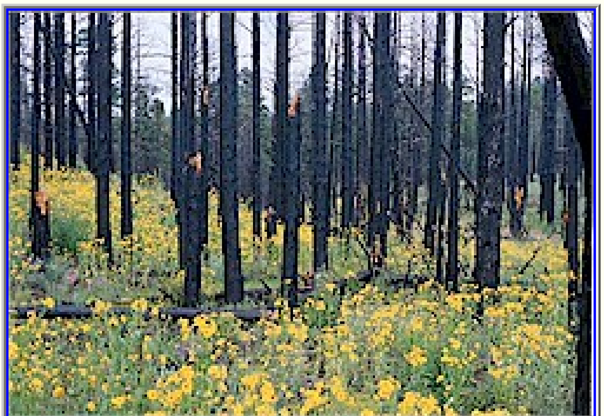
in Arizona and New Mexico oscillated between a few thousand acres to 60,000 acres annually. This yearly amount is dependent on local factors such as weather and fuel loads on the forest floor. However, beginning in 1992 the amount of acres burned between the two states has skyrocketed, with over 180,000 acres burning in 1997. Prior to fire suppression, the fires in the pine forests of the region behaved in a somewhat predictable manner determined by years of evolution and natural processes. The forest ecosystem of today, in contrast, has possibly reached a point of unstable criticality. A lightning strike may lead to a few trees burning, a few acres burning, or a catastrophic stand-replacing fire sweeping over thousands of acres of forest. Land managers and scientists are no longer able to predict with much confidence what direction fires in the ponderosa pine forests of the Colorado Plateau and the whole Southwest might take.



Aftermath of the high severity Hochderffer wildfire near the San Francisco Peaks, Arizona. Photo by Julie Crawford.

Fire control personnel with the United States Forest Service and other land management agencies are concerned that more fires might be dangerous, catastrophic fires until fuel loads are reduced below the critical threshold. Extensive tree-thinning projects and prescribed burning are two steps forest managers are taking to try to decrease the danger of high-intensity fires as well as restore the ponderosa pine forests of the region to a more "natural" state.

Despite the bleak appearance of charred black sticks following a major crown fire, native organisms and plants often quickly invade the site and recovery is underway. However, in many areas following these burns invasive species are able to establish themselves, crowding out native species.

Follow this link to:
Reintroduction of Fire to Forest Ecosystems

Research:

Fire-Southern Oscillation Relations in the Southwestern United States. A close linkage between fire and climate could diminish the importance of local processes in the long-term dynamics of fire-prone ecosystems. The structure and diversity of communities regulated by fire may have nonequilibrial properties associated with variations in global climate. Successful prediction of vegetation change hinges on a better understanding of climatically driven disturbance regimes and the relative contributions of regional versus local processes to community dynamics. Adapted from a journal article by Thomas W. Swetnam and Julio L.

Betancourt.

Restoring Ecosystem Health in Ponderosa Pine Forests of the Southwest.
Restoration of ecosystem structure and reintroduction of fire are necessary for restoring rates of decomposition, nutrient cycling, and net primary production to natural, presettlement levels. The rates of these processes will be higher in an ecosystem that approximates the natural structure and disturbance regime. Adapted from a published journal article by W. Wallace Covington *et al*.

Changed Southwestern Forests: Resource effects and management remedies.
Over 150 years of occupancy by northern Europeans has markedly changed vegetative conditions in the Southwest. Less fire due to grazing and fire suppression triggered a shift to forests with very high tree densities, which in turn contributed to destructive forest fires. Options to deal with these changes include prescribed fire, thinning and timber harvest to mimic natural disturbances and conditions. However, there are barriers to implementing these activities on a scale large enough to have a significant benefit. Adapted from a published journal article by Marlin Johnson.

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Biota

Biotic Communities

Alpine Tundra
Subalpine Conifer Forest
Quaking Aspen Forest
Mixed Conifer Forest
Ponderosa Pine Forest
Montane Chaparral/ Scrub
Pinyon-Juniper Woodland
Mountain Grasslands
Semi-arid Grasslands
Mountain Wetlands
Riparian Areas
Paleocommunities
Elevational Range
Merriam's Life Zones

Changes in the Biota

Endangered Species
California Condor
Endangered Fish
Mammal populations
Megafaunal Extinction
Invasive/Exotic Species
Forest Composition
Species Range Expansion
Species Extirpations
Status and Trends of

Exotic Tamarisk on the Colorado Plateau

Biota

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Saltcedar or Tamarisk (Tamaricaceae: *Tamarix ramosissima* Deneb)

Tamarisk trees grow in thick stands along the Little Colorado River near Cameron, AZ. Photo by John Grahame.

Deciduous, pentamerous saltcedar is a small, exotic tree introduced to the Southwest near the turn of the century from southern Eurasia (Horton 1977; Baum 1978). Saltcedar, now a dominant riparian shrubby tree in the Colorado River basin below 2,000 m elevation, spread rapidly throughout the system via wind-dispersed seeds (Graf 1978). Although saltcedar had reached the Grand Canyon by 1938 (Clover and Jotter 1944), the oldest trees found in the system thus far, date to about 1943 (Hereford personal communication; Stevens, in preparation). Saltcedar occupied pre-dam terraces and tributaries during the pre-dam era, and was the first species to invade the newly stabilized post-dam riparian zone in the Grand Canyon (Turner and Karpiscak 1980).

Mature saltcedar plants are capable of producing 2.5 x 10^8 tiny, wind-dispersed seeds per year (Stevens, in press). Its seeds are short-lived (less than 2 months in summer), have no dormancy requirements, and germinate in less than 24 hr. Saltcedar seeds require a moist, fine-grained (silt or smaller particle size) substrate for ecesis, such as is found in southwestern riparian habitats after flood waters subside (Stevens 1989a, b). Saltcedar commonly co-occurs with *Populus fremontii* (Fremont cottonwood), *Salix exigua* (sandbar or coyote willow), *Salix gooddinggii* (Goodding's willow), and *Tessaria sericea* (Marks 1950; Stevens, in press), but the non-native species is more tolerant of harsh environmental extremes than are native species (Warren and Turner 1975; Stevens and Waring 1985; Stevens, in press).

Saltcedar’s success in riparian environments in the Southwest appears to be a function of its phenomenal reproductive output and its greater drought and flood tolerance, as

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[Agents of Biotic Change](#)

Tamarisk in the lower Grand Canyon. These exotic trees are used by river runners for shade on river beaches. Photo by Bill Belknap, courtesy of Cline Library Special Collections, NAU.

compared to *Salix exigua* (Warren and Turner 1975; Stevens and Waring 1985). In an effort to understand the ecological success of saltcedar, experiments on its competitive ability, germination and nutritional requirements, and other aspects of its life history were conducted (Stevens 1986a). Competition experiments with *Salix exigua*, a common neighbor throughout the Colorado River system, failed to demonstrate competitive superiority of saltcedar over the willow. In fact, at the seedling stage, willow was competitively dominant.

Saltcedar was consumed by several introduced invertebrate herbivores, particularly the cicadellid leafhopper, *Opsius stactogalus*; however, invertebrate herbivore standing crop was equivalent with *Salix exigua* during normal (non-flooding) years in the Grand Canyon (Fig. 20; Stevens 1985). Saltcedar was more drought tolerant and inundation tolerant than any native species. Some saltcedar survived more than two years of root-crown inundation in the Grand Canyon during high water events from 1983-85 (Stevens and Waring 1988), a period far exceeding the 90 day record observed in warm, anoxic reservoir waters by Warren and Turner (1975). Saltcedar is extraordinary not only in its persistence, but also in its reproductive output, as mentioned, and seedling densities in excess of 16,000/m^2 have been observed in the southwest (Warren and Turner 1975). These life history characteristics make saltcedar highly successful in the harsh, unpredictable channels of unregulated southwestern rivers, but limit its recruitment along the more stabilized channels of regulated streams.

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